THE INFLUENCE OF SEASONALITY ON BRAIN SIZE EVOLUTION IN PRIMATES

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Zusammenfassung

Zahlreiche Theorien versuchen zu erklären, weshalb Tiere so unterschiedlich grosse Gehirne haben relativ zu ihrer Körpergrösse. Eine allgemein verbreitete Hypothese betont die Fitnessvorteile, welche verbesserte kognitive Fähigkeiten mit sich bringen, und argumentiert, dass ein starker Selektionsdruck bestehen muss, um die Kosten einer Vermehrung des metabolisch teuren Gehirngewebes zu überwinden. Eine neuere Hypothese, das „Expensive Brain Framework", postuliert hingegen, dass energetische Einschränkungen zu Unterschieden in der Gehirngrösse führen, da diese auf ökologischen Bedingungen beruhen, die mehr variieren als die allgegenwärtigen Vorteile verbesserter kognitiver Fähigkeiten. Dieser Ansatz besagt, dass in einem evolutionären Rahmen relativ grössere Gehirne nur dann entstehen können, wenn zusätzliche Energie zur Verfügung steht. Entweder wird dazu der der totale Energieumsatz erhöht, oder die Energie wird anderen Funktionen entzogen, oder beides. Die vorliegende Doktorarbeit benutzt diesen energetischen Ansatz, um die Beziehung zwischen ökologischen Bedingungen und relativer Gehirngrösse zu untersuchen, und zwar insbesondere die Effekte von Saisonalität. Eine neue Kompilation von Schädelvolumen und Körpergewichten nichtmenschlicher Primaten, deren saisonalen Diäten und der Saisonalität ihres Lebensraums wird mit modernen phylogenetischen Methoden untersucht. Klimavariablen und Pflanzenproduktivität wurden aus einer weltweiten Datenbasis entnommen.

Saisonalität, das periodische Auftreten von Nahrungsknappheit, kann entweder als eine kognitive Herausforderung angesehen werden oder aber als energetische Einschränkung. Der energetische Ansatz postuliert eine negative Beziehung zwischen Saisonalität und relativer Gehirngrösse, da das Gehirn eine ununterbrochene Energieversorgung braucht. Folglich wird die Gehirngrösse durch saisonale, unvermeidbare Hungerperioden eingeschränkt. Die „Cognitive Buffer"-Hypothese hingegen postuliert eine positive Beziehung zwischen Saisonalität und relativer Gehirngrösse, da die räumliche und zeitliche Futterverteilung in saisonalen Habitaten eine kognitive Herausforderung darstellt und demzufolge die Fitnessvorteile eines leistungsfähigeren Gehirns begünstigt. Einer der wichtigsten Beiträge dieser Doktorarbeit ist es zu zeigen, dass diese beiden Hypothesen sich nicht gegenseitig ausschliessen, sondern beide auf Primaten zutreffen. Die Hypothesen können als zwei Prozesse betrachtet werden, die zur selben Zeit agieren. Um diese Prozesse zu isolieren und nachzuweisen, muss man die energetischen Kosten von Zeiten herrschender Futterknappheit getrennt von den kognitiven Effekten

untersuchen, indem man zuerst bestimmt, wie sehr die Energieaufnahme über das Jahr hinweg fluktuiert (wie stark das Tier die Saisonalität empfindet), und danach feststellt, ob die tatsächliche Energieaufnahme stabiler ist als aufgrund der Fluktuationen in der Futterverfügbarkeit zu erwarten wäre. Wir zeigen mit Hilfe dieses Ansatzes, dass Primaten mit kleineren Gehirnen im Allgemeinen mehr Fluktuationen in ihrer Energieaufnahme ausgesetzt sind. Dies beweist, dass energetische Einschränkungen mit der relativen Gehirngrösse korrelieren. Andererseits konnten wir auch zeigen, dass Primaten mit grösseren Gehirnen ihre Energieaufnahme durch kognitive Fähigkeiten ausgleichen. Jedoch gibt es dabei Unterschiede zwischen den unterschiedlichen Primatengruppen: Lemuren zeigen eine schwächere Tendenz zum kognitiven Ausgleich als die Alt- und Neuweltaffen. Zusätzlich untersuchten wir, unter welchen Bedingungen ein solcher kognitiver Ausgleich bevorzugt stattfindet, und konnten zwei erklärende Faktoren identifizieren. Erstens muss die Umgebung ein gewisses Mass an Saisonalität aufweisen, und zweitens ist der Effekt bei Primaten, die sich hauptsächlich folivor ernähren, weniger häufig (sogar wenn wir für ihre insgesamt kleinere Gehirngrösse statistisch kontrollieren).

Zusammenfassend zeigt die vorliegende Doktorarbeit, dass ein energetischer Ansatz in Bezug auf ökologische Bedingungen einen beachtlichen Teil der Variation in der Gehirngrösse bei nichtmenschlichen Primaten zu erklären vermag. Dies bestätigt eine energetische Perspektive auf die Hirngrössenevolution, und ist ein erfolgreiches Beispiel dafür, wie die Kosten- und die Nutzenperspektive integriert werden können, um die Evolution unterschiedlicher Gehirngrössen zu verstehen. Weitere Studien werden auch davon profitieren, ökologische Bedingungen als einen Hauptfaktor in der Evolution von Gehirngrösse zu berücksichtigen.

Abstract

Many theories have been put forward to explain why there is so much variation in relative brain size among animals. The most prominent of these theories focus on the fitness benefits of having enhanced cognitive abilities, arguing that a strong selective pressure is needed to overcome the costs of an increase in the metabolically expensive brain tissue. The recently developed Expensive Brain framework, on the other hand, tries to explain variation in brain size as a consequence of the energetic constraints, which are supposed to vary more due to ecological conditions than the more ubiquitous fitness benefits. It states that relatively larger brains can only evolve if additional energy was obtained either by increasing total energy throughput, by reducing the energy allocation to other functions, or by a combination of both. In this thesis, this energetic approach is applied to investigate the relationship between ecological conditions and relative brain size, by looking at correlations with seasonality (periodic unavailability of food resources). Phylogenetic comparative methods are applied to a new, large compilation of primate endocranial volumes, body mass, seasonal patterns of diet and the seasonality of their habitat, extracted from a worldwide database of climate and plant production parameters.

Seasonality can be seen as either a cognitive challenge or an energetic constraint. The Expensive Brain framework predicts a negative relationship between seasonality and relative brain size, because brains need a continuous energy supply, and thus brain size is constrained by periods of unavoidable starvation which arise through seasonality. The Cognitive Buffer hypothesis predicts a positive relationship between seasonality and relative brain size, because spatiotemporal food distribution in seasonal habitats poses cognitive challenges and would therefore promote the fitness benefits of encephalization. One of the most important contributions of this thesis is to show that the two hypotheses are non-exclusive, and both apply in primates. They can best be seen as two processes which may operate at the same time. The key to distinguish between them is to consider the energetic costs of periods of food scarcity (by assessing how much energy intake fluctuates over the year, and thus the seasonality experienced by the animal) separately from the cognitive buffer effects (by looking at whether the energy intake fluctuates less than would be expected from fluctuations in food availability). Using this approach we show that smaller-brained primates in general experience more fluctuation in their energy intake than larger-brained primates, indicating a general energetic constraint of periods of food availability on brain size. But we find also that larger-brained primates cognitively buffer

their environment more. However, the degree to which cognitive buffering takes place differs between the different primate groups: lemurs show a weaker trend than the Old and New World primates. In addition, we test under which conditions cognitive buffering is facilitated, and identify two predictors for the amount of cognitive buffering. First, a certain degree of habitat seasonality needs to be present, but second we also found that largely folivorous primates show less cognitive buffering than frugi/omnivorous primates, even after controlling for their overall smaller brain size.

In conclusion, this thesis demonstrates that an energetic approach on ecological conditions can explain a considerable amount of brain size variation in primates, supporting an energetic cost perspective. Further research will profit from considering ecology as a major factor in brain size evolution, but also from this successful example on how to integrate cost- and benefit-perspectives to explain brain size evolution.

Chapter 1.

General Introduction

Theories on brain size evolution

The evolution of brain size has been a longterm focus of research for many reasons. One of these is the great variation in brain size between different vertebrate groups (Figure 1.1). The polygons enclosing data from species of each taxonomic group show not only that brain size varies considerable *between* the groups (there are clear grade shifts), but also that there is quite some variation among the species *within* each group. Furthermore, there is a general evolutionary trend towards a larger brain size, both in absolute terms and after controlling for body size, known as Marsh's rule (Jerison 1973). For example, birds and mammals are thought to have evolved from primitive reptiles, but their brain size polygon lies completely above that of the reptiles. Mammals have the largest brains relative to their body size, although the small mammals overlap with birds.

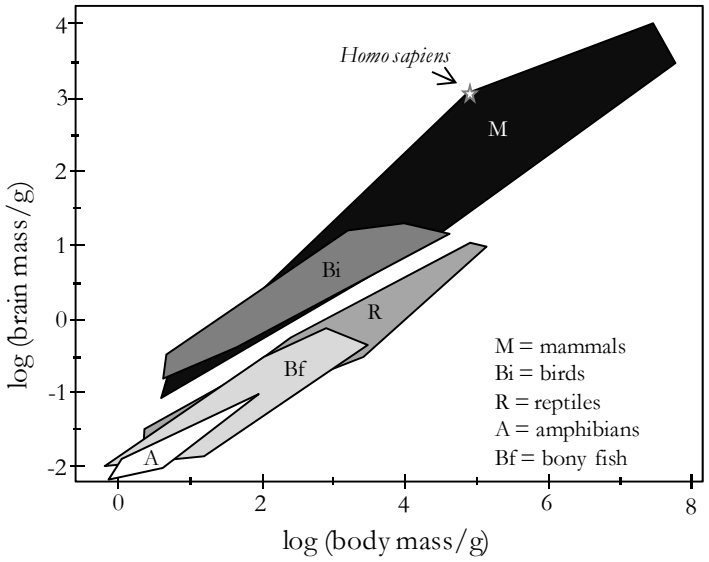

Figure 1.1. Brain and body relationship in vertebrates. Each minimum convex polygon represents a taxonomic group, formed by brain and body size data from several species within that group. Modified from Jerison 1973.

Brain size increases with body size, but in an allometric manner, rather than isometrically. This means that vertebrates with a larger body size have proportionally smaller brains than those with a smaller body size. Therefore, if we are interested in explaining the observed variation in brain size, we must correct for this allometric relationship with body size. This can be done by calculating relative brain size from the empirical regression of brain versus body size for the group of interest and taking the residuals, producing a measure known as encephalization quotient (observed / expected brain size) introduced by Jerison (1973) This residual brain size is then hypothesized to be a rough estimate of the intelligence of an animal. However, Deaner et al.(2007) showed that within primates, this assumption is incorrect. They found that overall brain size, or residuals from an intraspecific regression slope (0.25), predicted global cognitive ability better than residuals from an interspecific regression of brain size on body size (slope 0.75).

Results of correlations between brain size and explanatory variables may change depending on how body size is corrected for. In this thesis, this problem did not arise because by using the method of phylogenetic correction (phylogenetic least square analyses, PGLS), we did not take residuals from a predetermined slopt. This method is necessary because common evolutionary history causes phylogenetic non-independence between taxa in cross-species analyses (Harvey and Pagel 1991).

Paleoanthropologists are interested in brain size evolution because humans evolved a brain size that is approximately three times larger than our closest relatives, the chimpanzees, which are similar in body size, in a relatively short time period. This increase reflects one of the most remarkable adaptations in human evolution: the strong reliance on cognitive solutions to environmental and social problems.

Not surprisingly, much of the research has focused on questions such as: Why is there so much variation in brain size among species? And why did brain size increase over time? The most common approach to answer this question is to focus on the conditions that favored enlarged brains. Because brain tissue is metabolically very costly to grow and to maintain (Mink et al. 1981; Laughlin et al. 1998), there needs to be a strong selective pressure to invest in increased encephalization. Larger brains are associated with enhanced cognitive abilities (e.g. Tomasello 1999; Deaner et al. 2007; Reader et al. 2011), therefore many studies have focused on the explanation of the presence of larger brains as a *necessity* to deal with cognitive challenges complexity of some sort, a few of which I discuss below.

A very popular hypothesis on why primates have such large brains compared to other mammals is the *Macchiavellian intelligence hypothesis* (Byrne and Whiten 1988), later renamed the *social brain hypothesis* (Sawaguchi 1992; Dunbar 1998), which states that larger brains evolved to deal with "social complexity". The main assumption of this hypothesis is that considerable brain capacity is necessary to recognize individuals and their social relationships, to learn to predict and manipulate the behavior of other individuals and to benefit from their knowledge (but see Whiten and Byrne 1997). The predictions of this hypothesis are often tested using group size, grooming clique size or presence of coalitions as proxies for social complexity (e.g. Dunbar 1992; Kudo and Dunbar 2001; Lindenfors 2005; Shultz and Dunbar 2007).

Other ideas have been proposed around the necessity to deal with ecological complexity. It has been suggested that primate intelligence was driven by "cognitive mapping skills" required to deal with the spatio-temporal variability of food availability (Milton 1988). It has been proposed that tracking the locations and ripeness of fruit items that are scattered more widely through the forest than leaves indicates a need for superior spatial and temporal learning abilities, and leaf-eaters therefore do not need such abilities (e.g. Gibson 1986; Milton 1988). This idea is supported by the observed smaller brains of folivorous primates compared to frugivorous species (Clutton-Brock and Harvey 1980). However, in bats those species feeding on insects, which are also difficult to find, have smaller brains than frugivorous species (Dechmann and Safi 2009), which is inconsistent with this idea. A different ecological challenge is assumed by the *technical intelligence hypothesis* (Byrne 1997) and the related *extractive foraging hypothesis* (Parker and Gibson 1979; Gibson 1990). These do not only focus on how food is distributed in the environment, but also how food is located and processed. To extract embedded, hidden food sources (such as nut cracking or digging for insects) often requires complex object manipulation and thus greater intelligence. In support of this hypothesis, all great apes show food extraction or processing techniques that are technically demanding in some way, whereas monkeys do not.

Finally, a group of researchers focuses on more general behavioral flexibility by collecting data on for example frequency of innovation, social learning or tool use to quantify domain-general cognitive abilities, which are correlated with brain size (Reader and Laland 2002; Lefebvre et al. 2004). This approach suggests that rather than purely social intelligence driving brain evolution, ecologically relevant cognitive abilities (extractive foraging, dietary breath, frugivory) and elements of cultural intelligence (social learning) are important parts of general intelligence (Reader et al. 2011).

Adaptive traits are those that provide a *net* benefit to the organism. Thus, the hypotheses discussed above ignore the fact that these benefits must outweigh the high costs of growing and maintaining enlarged brains. Brain tissue is among the metabolically most costly tissues of the body, and its energy consumption cannot be temporarily reduced without permanent damage (Lukas and Campbell 2000). The *Expensive Brain framework* (Isler and van Schaik 2009a), based on previous hypotheses (Martin 1981; Armstrong 1983; Hofman 1983; Aiello and Wheeler 1995), states that growing and maintaining an enlarged brain is possible through two complementary pathways; (1) a stable increase in total energy intake or (2) reallocation of energy from either maintenance or production (growth and reproduction). However, while an adequate energy supply is a necessary precondition for increased encephalization, it is not a sufficient one. The expensive brain framework does not specify which selective benefit favored brain enlargement, and is in principle compatible with any of the benefit hypotheses listed above. However, if the costs are limiting and benefits are ubiquitous, i.e. reliable present in all species regardless of their ecology or social organization, accounting for the costs of brain enlargement would fully explain the taxonomic variation in relative brain size.

Tests of the predictions of the expensive brain framework have been very successful so far. Indeed, there is a significant positive relationship between relative brain mass and relative basal metabolic rate (BMR) in mammals, explaining 23% of brain size variation in primates (Isler and van Schaik 2006b; Isler et al. 2008), supporting the first possible pathway of increasing total energy intake to support a larger brain. In concurrence with the second pathway, energy allocation away from production is associated with larger brains. It has been well established that in all mammals (Isler and van Schaik 2009a), marsupials (Isler 2011) and birds (Isler and van Schaik 2006a) there is a strong trade-off between reproductive potential and brain size. Prolonged lifespan compensates the reduced fertility of relatively large-brained species, but this compensation is incomplete. Therefore Isler and van Schaik (2009b) suggest there is a "gray ceiling", beyond which maximum reproductive rate is so low that the risk of further brain expansion is very high (Cole 1954). The costs of reproduction can be reduced, however if energetic help is received through help from males or other group members, as in cooperative breeding (Isler and van Schaik, in prep, see also Isler 2011 for marsupials). The only part of the expensive brain framework that is not supported is the *expensive tissue hypothesis* (Aiello and Wheeler 1995). In birds (Isler and van Schaik 2006a), bats (Jones and MacLarnon 2004), and mammals generally (Navarrete et al. in rev.) there is no evidence for energetic trade-off between

the size of the brain and that of the gut size (or any other expensive organs), although in birds there is a trade-off between brain size and pectoral muscle mass (Isler and van Schaik 2006a) and in mammals between brain size and adipose depots mass (Navarrete et al., in rev). In sum, these findings show that in order to evaluate potential selective advantages of relatively large brains, energetic costs must not be neglected. However, an integration of the costs and benefits aspects has not been undertaken so far.

In this thesis I expand the energetic perspective on brain size evolution by focusing on ecology. In particular, I studied the influence of seasonality on brain size evolution in primates. Ecological influences on brain size evolution have received relatively little attention. A relevant hypothesis focusing on the benefits of ecological conditions is the *cognitive buffering hypothesis* (Allmann et al. 1993), alternatively termed *"brain size–environmental change" hypothesis* (Sol et al. 2008), which states that brain enlargement provides a survival advantage when facing novel challenges or with environmental complexity (elaborated below). This idea is supported mainly by studies on birds (Sol and Lefebvre 2000; Shultz et al. 2005; Sol et al. 2005a; Sol et al. 2007; Sol et al. 2008), but the few studies in primates found conflicting results in Anthropoid primates. MacDonald (2002) found a positive correlation between innovation frequency and seasonal variability, but further analyses did not confirm this result (Reader and MacDonald 2003). Here I complement this benefits approach with one that examines the costs of maintaining large brains in habitats with seasonal fluctuations of food availability.

Dealing with seasonal habitats

Seasonality is the phenomenon of recurrent fluctuations in climatic conditions and thus plant productivity. All animals have to deal with changing seasons to a greater or lesser degree; highly seasonal habitats force them to deal with periods of food scarcity. If an animal lives in a relatively non-seasonal habitat and its energy intake (experienced seasonality) follows the availability of its preferred food sources (the environmental seasonality), the net energy intake is likely to always remain above the minimal energetic need to maintain brain size (Figure 1.2A). This minimal energetic need is constant, as the brain is sensitive to starvation (Lukas and Campbell 2000) and therefore its energy needs cannot be temporarily reduced. If the seasonality of the environment is high and the available energy from preferred food sources drops below this minimal energetic need, there is a period of negative energy balance that needs to be dealt with

(grey zone in Figure 1.2B). There are two possible and complementary ways in which this can be done. The first is to decrease brain size, and thereby to lower the minimal energetic need to the lowest point in the lean period (Figure 1.2C). Another strategy is to buffer the environmental seasonality by keeping the net energy intake more constant throughout the year (Figure 1.2D). This may be achieved by either decreasing energy *expenditure* or by increasing energy *intake*. Examples of the first buffering tactic are decreased activity, seasonal breeding or fat storage. These types of buffers we term "physiological buffers" and we do not expect them to help maintain brain size in periods of unavoidable starvation. Alternatively, cognitive abilities facilitate increasing energy intake through for example finding other (hidden) food sources in periods where the preferred food items are scarce, therefore we term leveling energy intake through behavioral changes "cognitive buffering".

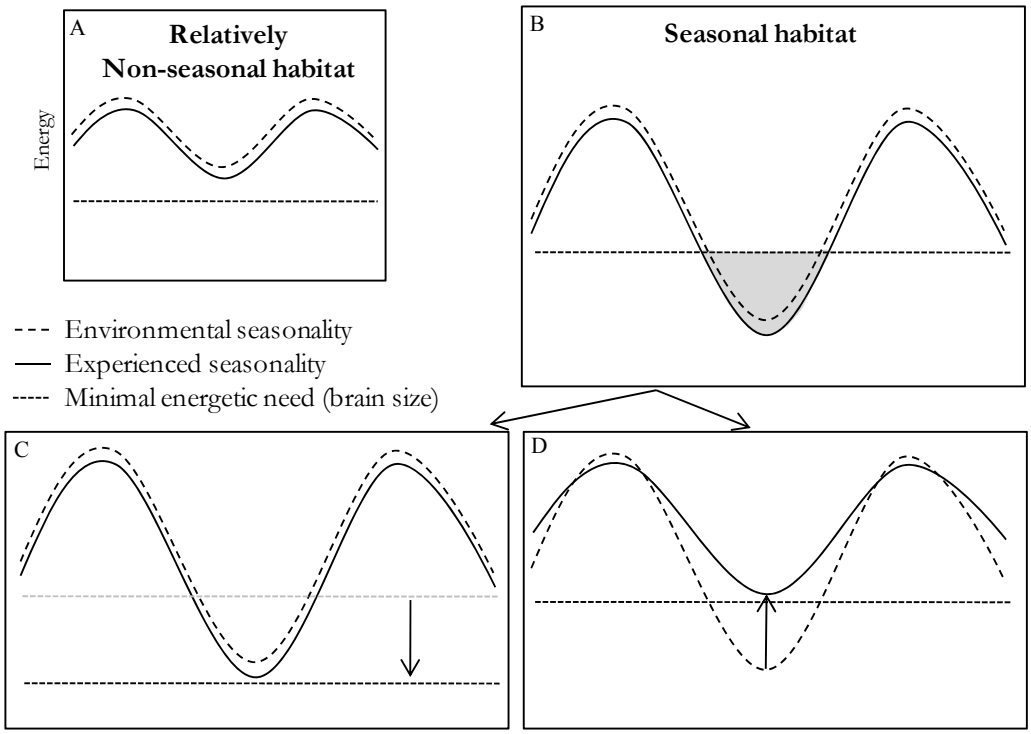

Figure 1.2. Energetic representation of living in a relatively non-seasonal (A) and a seasonal habitat (B-D). If in a seasonal habitat the energy available in the preferred food resource (depicted as environmental seasonality) falls below the minimal energetic need (grey area B), there are two possible ways of dealing with this. Either the minimal energetic needs, thus brain size, can be decreased to the lean period (C), or seasonality can be buffered by keeping net energy intake more constant throughout the year (D).

Testing two hypotheses

The two strategies of dealing with seasonal habitats are representations of two hypotheses that are central throughout this thesis. The first is the Expensive Brain hypothesis (Isler and van Schaik 2009a). As mentioned earlier, this hypothesis states that in order to pay for an enlarged brain, energy needs to be made available from either an increased energy intake or from changes in energy allocation. For the purpose of this thesis, we utilize this framework stating that periods of unavoidable starvation caused by seasonality decreases energy input and thus impose a reduced brain size to decrease energy needs (top path Figure 1.3). It is important to note that seasonality needs to be assessed from the animal's perspective by looking at how its energetic intake varies over the year, i.e. its "experienced" seasonality. This hypothesis then predicts a negative relationship between relative brain size and the degree of experienced seasonality.

The second hypothesis is the Cognitive Buffer hypothesis (Allmann et al. 1993; Deaner et al. 2003; Sol 2009). This hypothesis focuses more on the ecological benefits of encephalization and states that larger brains provide the cognitive abilities to behave flexibly, which facilitate buffering seasonality (bottom path Figure 1.3). In order to measure how much cognitive buffering is actually taking place we cannot, however, merely look at experienced seasonality or habitat seasonality. As explained above, those animals that cognitively buffer the seasonality in their habitat will experience less fluctuation in their energetic intake than is expected from the fluctuation in the habitat. Therefore, this hypothesis predicts a positive relationship between relative brain size and the difference between environmental and experienced seasonality (bottom path Figure 1.3).

In this thesis I will show that these two hypotheses are not mutually exclusive. Indeed, they may profitably be seen as two processes that operate simultaneously; on the one side the effects of energy costs and on the other those of cognitive buffering. Intrinsic (e.g. life history) and extrinsic (e.g. habitat) factors determine their relative importance in a lineage.

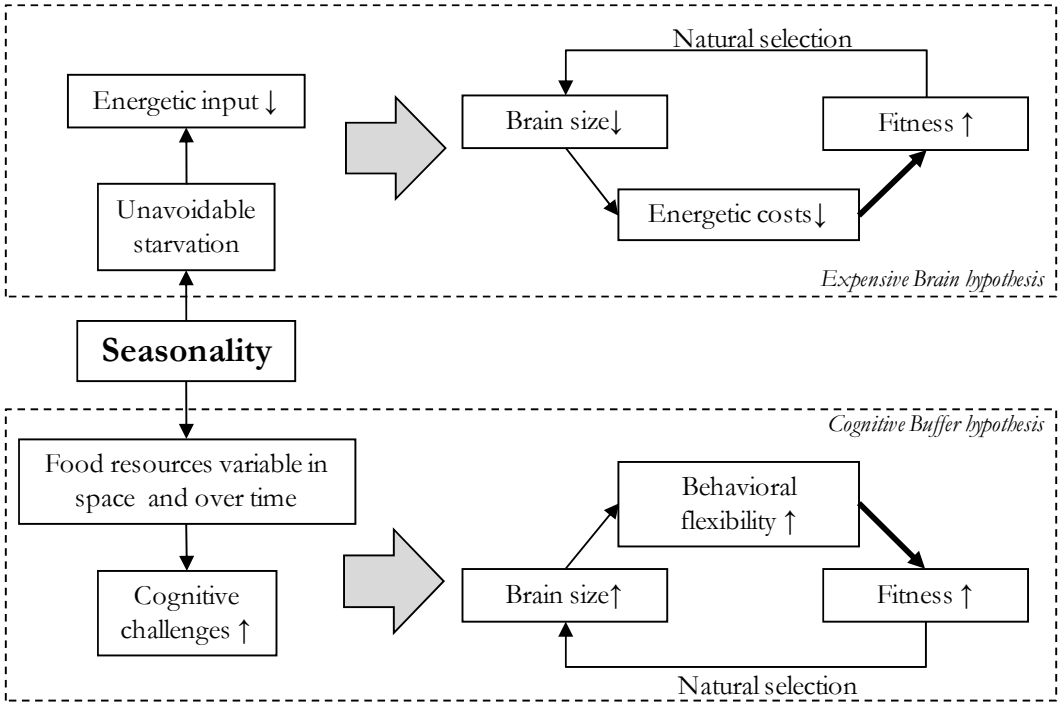

Figure 1.3. Pathways of two central hypotheses to explain how seasonality affects brain size evolution. The Expensive Brain hypothesis predicts that the unavoidable starvation induced by seasonality forces brain size to decrease because energy input is lowered. The Cognitive Buffer hypothesis, on the other hand, predicts that animals with an enlarged brain have increased fitness, because this larger brain helps them cope better with the cognitive challenges imposed by seasonal habitats (modified from Isler and van Schaik 2009a; Sol 2009).

By investigating these two effects in primates, I aim to demonstrate that ecological factors determine costs and benefits of brains, which both act as selective pressures on brain size evolution. With this approach, we will be able to explain why the above-mentioned general trend of brain size increase over time is constrained to a different degree in various lineages, or even reversed under certain conditions, such as small islands (Köhler and Moyà-Solà 2004; Niven 2005; Safi et al. 2005; Boerner and Krüger 2008; Weston and Lister 2009; Montgomery et al. 2010).

Organization of this thesis

In the second chapter, I test the predictions of these two hypotheses, the Expensive Brain hypothesis and the Cognitive Buffer hypothesis, in the African strepsirrhine primates. The lemurs make a great study example, because they live on a large island with a pronounced gradient of seasonality, the east being far less seasonal than the west. Both African lorises and the Malagasy lemurs showed a direct negative relationship between environmental seasonality and relative brain size. Those that lived in more seasonal habitats had relatively smaller brains, supporting the hypothesis of an energetic constraint on brain size in both groups. The Cognitive Buffer hypothesis could only be tested in the Malagasy lemurs, as there was very limited dietary data available for the African lorises. We only found a weak cognitive buffering effect in this group of primates.

In the third chapter, we extend the tests of these hypotheses to the largest primate group; the non-human catarrhine primates. This diverse group consists of Old World monkeys and apes, ranging from Africa to South-East Asia. Besides the great variation in the amount of environmental seasonality, this group also varies greatly in the way they deal with it; therefore, measuring seasonality from the animal's perspective was very important. In this group the conjunction of energetic costs and cognitive buffering became apparent. We found a strong negative influence of experienced seasonality on relative brain size and also a strong positive influence of cognitive buffering on relative brain size. Because the effects of both energetic constraints and cognitive buffering were roughly equally strong, they cancelled each other out, leaving no direct correlation between environmental seasonality and relative brain size.

The fourth chapter then explores various factors that may predict the evolution of cognitive buffering in primates. For this we first demonstrated that the last group of primates, the New World primates (platyrrhines), showed a very similar pattern in the influence of seasonality on brain size as the catarrhine primates. In both anthropoid groups we found equally strong effects of both energetic constraints and of cognitive buffering, leaving no direct correlation between environmental seasonality on relative brain size. Investigating potential factors that facilitate cognitive buffering, we found that specialized folivores seem to be limited in their ability to cognitively buffer the seasonality of their habitat, even if the general effect of the

relatively smaller brains of folivore primates is controlled for statistically. In addition, our results indicate that cognitive buffering is facilitated in more seasonal habitat, but only up to a certain degree of habitat seasonality. If the habitat is very seasonal, either in the amount of plant productivity or in temperature, cognitive buffering is no longer feasible, and physiological buffers such as hibernation or fat storage are needed. There results indicate the importance of taking ecological constraints into account in explaining the evolution of brain size.

Finally in the discussion I put the findings of this project into perspective with previous studies, discuss the limitations of this work, and I suggest some possible future directions for research, especially with regard to the integration of cost and benefit approaches.

Chapter 2.

Effects of Seasonality on Brain Size Evolution: Evidence from Strepsirrhine Primates

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Abstract

Seasonal changes in energy supply impose energetic constraints that affect many physiological and behavioral characteristics of organisms. As brains are costly, we predict brain size to be relatively small in species that experience a higher degree of seasonality (Expensive Brain framework). Alternatively, it has been argued that larger brains give animals the behavioral flexibility to buffer the effects of habitat seasonality (Cognitive Buffer hypothesis). Here, we test these two hypotheses in a comparative study on strepsirrhine primates (African lorises and Malagasy lemurs) that experience widely varying degrees of seasonality. We found that experienced seasonality is negatively correlated with relative brain size in both groups, controlling for the effect of phylogenetic relationships and possible confounding variables such as the extent of folivory. However, relatively larger-brained lemur species tend to experience less variation in their dietary intake than indicated by the seasonality of their habitat. In conclusion, we found clear support for the hypothesis that seasonality restricts brain size in strepsirrhines as predicted by the Expensive Brain framework, and weak support for the Cognitive Buffer hypothesis in lemurs.

Introduction

Many physiological and behavioral adaptations of animals reflect characteristics of their habitats. Indeed, it is known that the variability of environmental conditions over time, or degree of seasonality of a habitat, influences traits such as body size, group size, group composition and home range size (e.g. Eeley and Foley 1999; Nunn 1999; Strier et al. 1999; Ostner et al. 2002; Lehman et al. 2005; Plavcan et al. 2005). However, there is neither much theory nor empirical information about the relationship between habitat seasonality and brain size. In this paper, we develop and test detailed predictions that arise from two hypotheses: the Expensive Brain framework and the Cognitive Buffer hypothesis.

First, considering that brain tissue requires a high and uninterrupted supply of energy (Mink et al. 1981) and building on earlier hypotheses about energetic constraints on brain size evolution (e.g. Aiello and Wheeler 1995), the Expensive Brain framework (Isler and van Schaik 2009a) proposes that an increase in brain size relative to body size is only possible if either total energy metabolism is increased, the energy allocation to other functions is reduced, or both. Since serious starvation leads to permanent brain damage (Lukas and Campbell 2000), we expect brain size to be constrained if in a seasonal habitat the energy supply is periodically low, even if physiological buffers such as fat storage, reduced activity, or hibernation allow survival. Frequently, animals change to fallback foods that are of lower dietary quality than the preferred diet, but are more abundant or not seasonally scarce (Hemingway and Bynum 2005). Such diet shifts also represent a physiological buffer, since the total net energy available per day is still reduced during the lean period, i.e. the animal still experiences the seasonality of its habitat. Each species is adapted to its preferred or staple diet morphologically. If it would be able to fully compensate (or even overcompensate) the change in diet during lean periods, e.g. by increasing foraging effort, and thus be better adapted to fallback foods, these foods would become its staple diet also during the good periods (as is the case in many folivorous primates). Of course, some differences in brain size may result from the main adaptation, and therefore it is important to control for diet type when testing the correlations between seasonality and brain size.

All physiological buffers entail a seasonally reduced energy budget, but the costs of brain function are not reduced (except probably in deeply hibernating rodents, Krilowicz et al. 1988). The central prediction of the Expensive Brain framework is therefore that, all other things being equal, the average brain size within a population is negatively related to the duration (and perhaps

frequency) of periods of low food availability that cannot be fully compensated by increased foraging effort. To test this prediction, we use the temporal variation in the consumption of the diet component with the highest nutritional value (i.e. preferred food item) as an index for the degree of variation in energy intake, henceforth referred to as experienced seasonality. To enhance comparability with other studies and to explore possibilities for future studies, we also investigate how well experienced seasonality is predicted by climatic variables - annual variation in rainfall and temperature (Janson and Chapman 1999) and a more direct measure of plant productivity, Normalized Difference Vegetation Index (NDVI, Pettorelli et al. 2005).

This prediction from the Expensive Brain framework enjoys some empirical support from a similar phenomenon, island dwarfism. Many mammals show dwarfing on small islands where high population densities may produce resource shortages (Filin and Ziv 2004; Lomolino 2005), especially in relatively large-bodied species (the opposite phenomenon, island gigantism, is found in relatively small species if predation pressure on an island is reduced but food resources are not limited). Köhler and Moyà-Solà (2004) suggested that dwarf island forms of a rupicaprine bovid (*Myotragus*) are relatively smaller-brained and linked the relative reduction in brain size to limited resources. Based on this, Niven (2007) discusses potential impacts of resource limitations on brain size in the hominin *Homo floresiensis*. Weston and Lister (2009) have made the same argument for *Hippopotamus* species on islands. Similarly, Taylor and van Schaik (2007) argued that a subspecies of Bornean orangutans living in a region with more frequent El Niño-induced droughts and forest fires is relatively smaller-brained because it is forced to feed largely on the nutritiously poor inner bark of trees more than other orangutans.

The second hypothesis predicts the opposite pattern. The Cognitive Buffer hypothesis (Allmann et al. 1993) assumes that relatively large brained species benefit from enhanced cognitive abilities. Seasonal habitats are likely to be more cognitively demanding than non-seasonal habitats because preferred food sources are more dispersed in space and over time. Larger-brained individuals would therefore perform better in seasonal habitats because their enhanced cognitive abilities will facilitate flexible behavioral responses to the fluctuating environment. Thus, we would expect selection to favor relatively large brains in seasonal habitats. This hypothesis is supported by a comparative study on Neotropical parrots, which found a positive correlation between climatic variability and brain size (Schuck-Paim et al. 2008). Moreover, migrating birds have smaller brains than non-migrating species (Winkler et al. 2004; Sol et al. 2005b), which the authors interpret as a cognitive buffer effect in the residential species.

The two effects may also operate in combination. If the energetic constraints, predicted by the Expensive Brain framework holds; the presence of a cognitive buffer effect would reduce the negative correlation between brain size and seasonality in energy availability. Thus, to test whether both cognitive buffer effects and energetic constraints operate, we look for a dampening of the environmental seasonality through increased energy intake. The combined Expensive Brain - Cognitive Buffer hypothesis predicts that in relatively large-brained species the seasonality experienced by the animals (i.e. temporal variation in energy intake) is far less than the seasonality of the environment they live in (Figure 2.1).

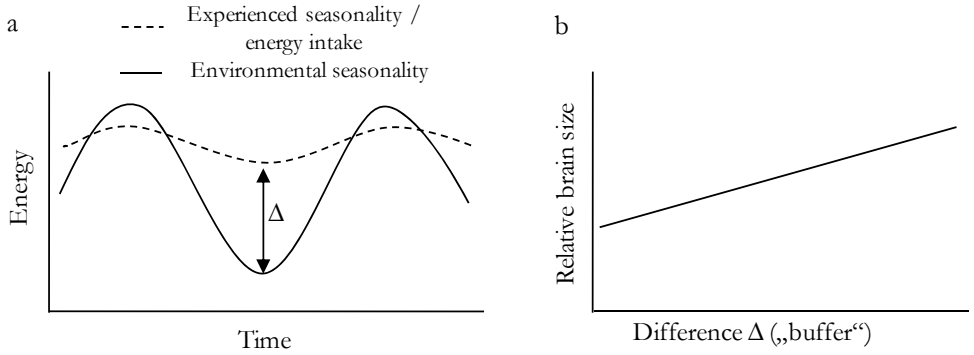

Figure 2.1. A large difference (Δ) between experienced and environmental seasonality would imply a large dampening effect ("buffer") through behavioral flexibility (a). Even if energetic constraints result in an overall negative correlation between relative brain size and experienced seasonality, cognitive buffer effects would result in a positive correlation between relative brain size and the difference between environmental and experienced seasonality (b).

In this study we test these predictions in two groups of strepsirrhine primates, the African lorises and the Malagasy lemurs. Both groups are of small to medium body size and more encephalized than the average mammal, and thus devote a relatively large percentage of basal metabolism to brain maintenance (11-12% as compared to 8-9% in cercopthecoid primates, calculated from Mink et al. 1981; Isler et al. 2008). Godfrey et al (2001) and Catlett et al. (2010) showed that age at weaning is positively (or dental precocity is negatively) correlated to brain

size in lemurs, but otherwise strepsirrhines do not exhibit the usual correlates of encephalization found in anthropoid primates, such as group size (Shultz and Dunbar 2007; MacLean et al. 2009) or diet quality (Fish and Lockwood 2003).

The lemurs are particularly interesting here as they are endemic to Madagascar, a large island with strong and varied climatic seasonality (Dewar and Richard 2007). The eastern part is characterized by high annual rainfall and a low degree of within-year climatic seasonality, which is struck in some years by extreme climatic conditions (storms and cyclones, see Ganzhorn 1995). The much larger western part is extremely seasonal within a year for such latitudes, but more predictable between years. In response, lemurs have evolved a great variety of special adaptations to cope with the seasonality of their environment (Ganzhorn et al. 1999; Wright 1999): almost all species show extreme birth seasonality (Janson and Verdolin 2005), the basal metabolic rates of most species are below those of haplorhine primates (Genoud 2002), and the only two species of primates that show torpor or hibernation are lemurs (Dausmann et al. 2004; Schülke and Ostner 2007). As lemurs are thus a highly diverse group of primates, it is necessary to test whether environmental seasonality is a good proxy for energy intake, or whether we must use more direct measure of experienced seasonality. If environmental seasonality and experienced seasonality differ, we can use the difference between the two to test whether relatively large-brained lemur species cognitively buffer the impact of their seasonal environment.

For African lorises, detailed data on monthly diet composition throughout the year are largely unavailable (Charles-Dominique 1974; Harcourt 1986); thus an analogous test is not possible. However, since all African lorises are nocturnal and arboreal and their diets are homogeneous and largely insectivorous (Rowe 1996), we assume that environmental seasonality directly reflects seasonality of energy intake in this group. Insect availability follows rainfall seasonality more than it does the production of new leaves (Wolda 1978; Coley and Barone 1996). Leaf production can differ considerably from rainfall if, as in Central Africa, plant productivity is not limited by rainfall but by irradiance (Wright and van Schaik 1994). We therefore assume that variation in rainfall and temperature, as a proxy for irradiance, are more reliable proxies for experienced seasonality than plant productivity in the African lorises.

Methods

Brain and body size

Endocranial volumes (ECV) were measured from 428 skulls using glass beads in eight European and four American museums and added to the dataset of Isler et al. (2008) to a total of 1049 skulls (from 507 known locations). Only adult specimens (third molar present) for whom the original provenance was known were included in our sample, in order to exclude a possible effect of captivity. In total, our sample comprises 934 adult individuals from 36 lemur species from 215 locations and 15 loris species from 241 locations (Table A2.4).

It has been documented that primates tend to have smaller body sizes in more seasonal habitats (Albrecht et al. 1990; Lehman et al. 2005; Plavcan et al. 2005). It is therefore important to include body size as a covariate in the analyses. Body masses from wild study populations were collected from literature sources (Table A2.4). In their monumental compilation of primate body masses, Smith and Jungers (1997) also included body weights from populations of the Duke Lemur Center (DLC) in Durham USA, but since there is a large captivity effect on body mass (Isler et al. 2008) we did not include studies on body weights from the DLC. Male and female body mass and endocranial volumes were pooled, since most strepsirrhine primates do not exhibit sexual dimorphism in body mass (if it exists, females tend to be slightly heavier, see Kappeler 1997).

For 7 out of 36 species no wild body mass data were available. Therefore, bitubular breadth and bizygomatic breadth of the skulls were used to estimate body mass (Plavcan 2003). Results did not differ in their level of significance if these species were excluded from the analyses, and therefore they were included.

Seasonality

Malagasy lemurs

In lemurs, we measure experienced seasonality by using temporal variation in the consumption of the diet component with the highest nutritional value. The dietary data were taken from Hemingway and Bynum (2005), with additional recent studies added (Table A2.4). In total, dietary data were available for 26 populations of 19 lemur species. The coefficient of variation (CV) in consumption of dietary components over a year was measured from the

monthly means of the following food items: insects, fruit/seeds, flowers, young leaves and mature leaves. From this, we calculated the CV in the item with the highest nutritional value eaten for more than 10% of the average feeding time (insects > fruit/seeds > flowers > young leaves > mature leaves), henceforth referred to as CV in diet. Second, the total nutritional value per month was calculated as the sum of each item times its quality (8 for insects, 5 for fruits, seeds, flowers, 3 for young leaves, 1 for mature leaves, Langer 2003), yielding a coefficient of variation of net energy intake. We assume that energy expenditure is equal throughout the year, since field metabolic rates are too insufficiently studied.

Ideally, we would use diet variability, brain and body mass of the same population for each lemur species. However, diet composition has generally been studied in different populations than the specimens available in museum from which brain sizes were measured. Therefore, we compiled values of brain and body mass sampled within a 100 km radius of the population in which diet composition was studied. However, results from an overall average of brain and body mass dataset (N=19) did not differ in their level of significance from results from this reduced conservative dataset (N=15); therefore all of our results presented here are based on the larger dataset.

We tested whether experienced seasonality matches environmental seasonality reflected by plant productivity and climatic seasonality. van Schaik and Pfannes (2005) showed that tropical primates living in climatically seasonal habitats experience seasonality in resource availability. In their study, three measures of precipitation variation correlate positively with flush/flower/fruit availability: first, the coefficient of variation (CV=Standard deviation (SD)/mean); second, the mean vector length (*r*) that estimates the concentration of precipitation over the year (Batschelet 1981); third, P2T as a measure of the length of the dry season, a dry month is defined when its total precipitation is less than two times the mean temperature (Walter 1971)[1]. We calculated these three seasonality measures (CV, *r* and P2T) from monthly precipitation means and standard deviation (SD) in temperature. In west Madagascar water is estimated to be the major limiting factor for plant production, whereas in east Madagascar irradiance is thought to be limiting plant productivity (Boisvenue and Running 2006). All these climatic seasonality measures were calculated from the WorldClim data base (Hijmans et al.

[1] P2T = number of dry months per year, with a dry month defined by precipitation (P; mL) < 2 x temperature (T; degrees C). For example, a month with a mean temperature of 30_C and less than 60 mL of precipitation will be considered dry.

2005) using ArcGIS 9.1. In addition, we extracted the Normalized Difference Vegetation Index (NDVI, see Myneni et al. 2005), a more direct measure of plant productivity, from the GIMMS database (Tucker et al. 2005) and calculated its seasonality using the coefficient of variation (CV).

African lorises

For lorises, diet composition data are not available in sufficient detail to study monthly variation (Charles-Dominique 1974; Harcourt 1986). Fortunately, however African lorises are homogeneous in their diet and lifestyle, and we therefore assume that environmental seasonality is a good proxy of experienced seasonality in this group. We calculated the same climatic measures as described above (CV in precipitation, *r* in precipitation, P2T – the number of dry months – and SD in temperature). However, in contrasts to the situation in Malagasy lemurs, plant productivity is probably not reflecting experienced seasonality in lorises, since in Equatorial Africa plant productivity does not correlate with insect availability (Wolda 1978; Coley and Barone 1996).

Analyses of brain size variation

First, we tested whether seasonality was an energetic constraint on brain size by examining the relationship between relative brain size and seasonality. In the lemurs, results of analyses using the CV of only highest nutritional value food item were very similar to those obtained using CV of net energy intake (dietary items times their quality). Hence, we only report the first set of results.

Additionally we performed a within-genus comparison in the lemurs, using residual brain sizes of each species from a brain against body mass regression within lemurs (Table A2.3). We compared the relative brain sizes from taxa inhabiting the western, more seasonal part of Madagascar with their sister taxa inhabiting the eastern, less seasonal part of Madagascar. We expected that the sister taxa living in the western part would have relatively smaller brains than the ones living in the eastern part.

Second, to test whether lemurs cognitively buffer seasonality, we examined the relationship between relative brain size and the difference between the seasonality of the habitat (CV in precipitation and CV in NDVI) and the seasonality in net energy intake (CV in dietary items times their quality). Here, taking the complete net energy intake into account is critical

since we are interested in how much buffering through feeding on fallback foods is taking place during the lean season.

We controlled for phylogenetic relatedness using PGLS analyses in R (R-Development-Core-Team 2010) with the CAIC package (Orme et al. 2009). Strepsirrhine relations are debated (Mittermeier et al. 2008), and therefore we ran all analyses with four different, recently suggested trees (Bininda-Emonds et al. 2007; Horvath et al. 2008; Orlando et al. 2008; Arnold et al. 2010). Results remained largely unaffected by the choice of phylogenetic tree (see Table A2.1). We therefore report only the results based on Horvath et al. (2008) (Figure A2.1), with the following species added according to their location and distances in version 2 of the consensus tree based on the Bayesian Primate phylogeny from the 10K Trees Project (Arnold et al. 2010): *H. alaotrensis*, *H. occidentalis, P. deckenii, P. verreauxi, P. edwardsi, A. occidentalis, A. laniger, I. indri, L. mustelinus, L. edwardsi, L. dorsalis, L. microdon, C. major and M. rufus*. Furthermore, *P. pallescens, P. furcifer* and *C. ravus* were added according to relations reported in Groves (2000) and Pastorini et al. (2001). Results did not differ if the latter three species were removed from the analyses; therefore they are included in the reported results. The loris phylogeny was based on version 2 of the consensus tree from the 10K Trees Project (Arnold et al. 2010) with *Galago thomasi, Galago matschiei, Otolemur monteiri* and *Euoticus pallidus* added according to Bininda-Emonds et al. (2007). As the parameter lambda was always close to 1, indicating a strong phylogenetic component in the data, we show independent contrast values in Figure 2.2. Brain and body variables were log-transformed before analysis, and statistical tests were parametric least-squares regressions, using JMP 7.0.2.

In all multiple regressions, body mass was included as a covariate, and residuals of brain size versus body mass are shown in graphs. Diurnality, degree of folivory and group size have been shown to correlate with brain size in primates (reviewed in Healy and Rowe 2007); hence we took these possibly confounding variables into account. Torpor or hibernation is the most extreme adaptation to cope with seasonal energy shortages, and is found only within two lemur genera, *Cheirogaleus* spp. and *Microcebus* spp. (review Schülke and Ostner 2007). Although it is unknown how the metabolic requirements of brain tissue are affected by torpor or hibernation in primates, these two genera are among the least encephalized of all primates and a possible relationship between periodic torpor and brain size can be expected. Therefore, we selected a model with the best fit according to the Information Theory Criterion (Akaike 1974) including the following possible co-variables: body mass, variability in diet, hibernation/torpor, diurnality

(nocturnal, diurnal, cathemeral), degree of folivory (yearly average percentage of leaves in the diet) and maximum group size.

Results

Experienced vs. environmental seasonality

We tested the predictive power of monthly variation in plant productivity and climate for experienced seasonality in the Malagasy lemurs. Only the coefficient of variation (CV) in plant productivity (Normalized Difference Vegetation Index, NDVI) and the concentration (*r*) in precipitation were significantly correlated with CV in diet (NDVI: r^2=0.31, p=0.014; *r* in precipitation: r^2=0.23, p=0.037), whereas the other measures of climatic seasonality showed only a trend or no significance (CV in precipitation: r^2=0.20, p=0.05; P2T (number of dry months): r^2=0.13, p=0.13; SD in temperature: r^2=0.03, p=0.48). The low coefficient of determination r^2 indicated that variation in plant productivity (CV in NDVI) and precipitation (*r* in precipitation) were rather weak predictors for experienced seasonality in the lemurs.

Seasonality as an energetic constraint on brain size

In lemurs, variation in diet was significantly negatively correlated with brain size (PGLS t=-3.35, p=0.004, λ=0.999; Figure 2.2a and 2.2b), indicating that lemur species with more variation in the consumption of their preferred food item have smaller brains. The best fit model according to the Akaike's Information Theory Criterion included body mass, CV in diet and group size with a significant influence of body mass and CV in diet (Table 2.1). The relationships between brain size and variation in precipitation and plant productivity were all negative for the lemurs, but only CV in plant productivity and length of dry season (P2T) showed a significant correlation (Table 2.1).

With our within-genus comparison in the lemurs, we confirmed that taxa inhabiting the western, more seasonal part of Madagascar evolved relatively smaller brains than their sister taxa living on the eastern side (Table A2.2). The effect is stronger within the smaller sister taxa (*Microcebus, Cheirogaleus*) than the larger ones (*Propithecus*).

In the African lorises, we found a significant negative correlation between relative brain size and all environmental variables, except length of dry season (P2T), where we found a strong trend (Table 2.1, Figure 2.2c and 2.2d). As expected, plant productivity and relative brain size were not correlated in this group.

Seasonality as a cognitive challenge

The negative correlations we found between relative brain size and experienced seasonality support the Expensive Brain framework. However, cognitive buffer effects, predicted by the Cognitive Buffer hypothesis, could still apply in addition to the energetic constraints; since within lemurs experienced seasonality, as proxied by temporal variation in energy intake, is not well predicted by environmental seasonality (see above). Therefore, we tested whether a combination of energetic constraints and cognitive buffer effects applied here. We found a positive trend between relative brain size and the difference between experienced seasonality and environmental seasonality (experienced seasonality - seasonality in plant productivity: N=19, species level: t=2.13, p=0.05, PGLS: p=0.14, λ=1.00; experienced seasonality - seasonality in precipitation: N=19, species level: t=1.83, p=0.09, PGLS: p=0.11, λ=1.00). We found no difference in the results when we controlled for possible confounding variables (hibernation / torpor, diurnality, degree of folivory and maximum group size).

Table 2.1. PGLS best fit models between relative brain size (corrected for body mass) and climatic seasonality in Malagasy lemurs and African lorises.

	Malagasy lemurs (climate: N= 36; diet: N=19)			**African lorises (N=16)**		
Seasonality measure	t- ratio	*P*	λ	t-ratio	*P*	λ
CV in diet	-3.35	**0.004**	1.00			
CV in plant productivity	-2.92	**0.007**	0.97	-0.32	0.757	0.72
r in precipitation	-0.94	0.355	0.95	-2.94	**0.011**	0.98
CV in precipitation	-0.91	0.368	0.95	-2.19	**0.047**	1.00
P2T	2.39	**0.023**	0.99	2.03	0.062	1.00
SD in temperature	-0.84	0.406	0.93	-2.65	0.020	1.00

Notes: For the lemurs, dietary type and hibernation are included in the bestfit model for the climatic seasonality measures. In the best-fit models for experienced seasonality (CV in diet), hibernation is included as a covariable (results remain the same if hibernation is excluded; see Table A3. Since the African lorises do not differ in dietary type or nocturnality and group size did not have an effect, the model included only brain size, body mass, and climatic seasonality. Significant *P* values are shown in boldface. All λ values are not significantly different from 0**.**

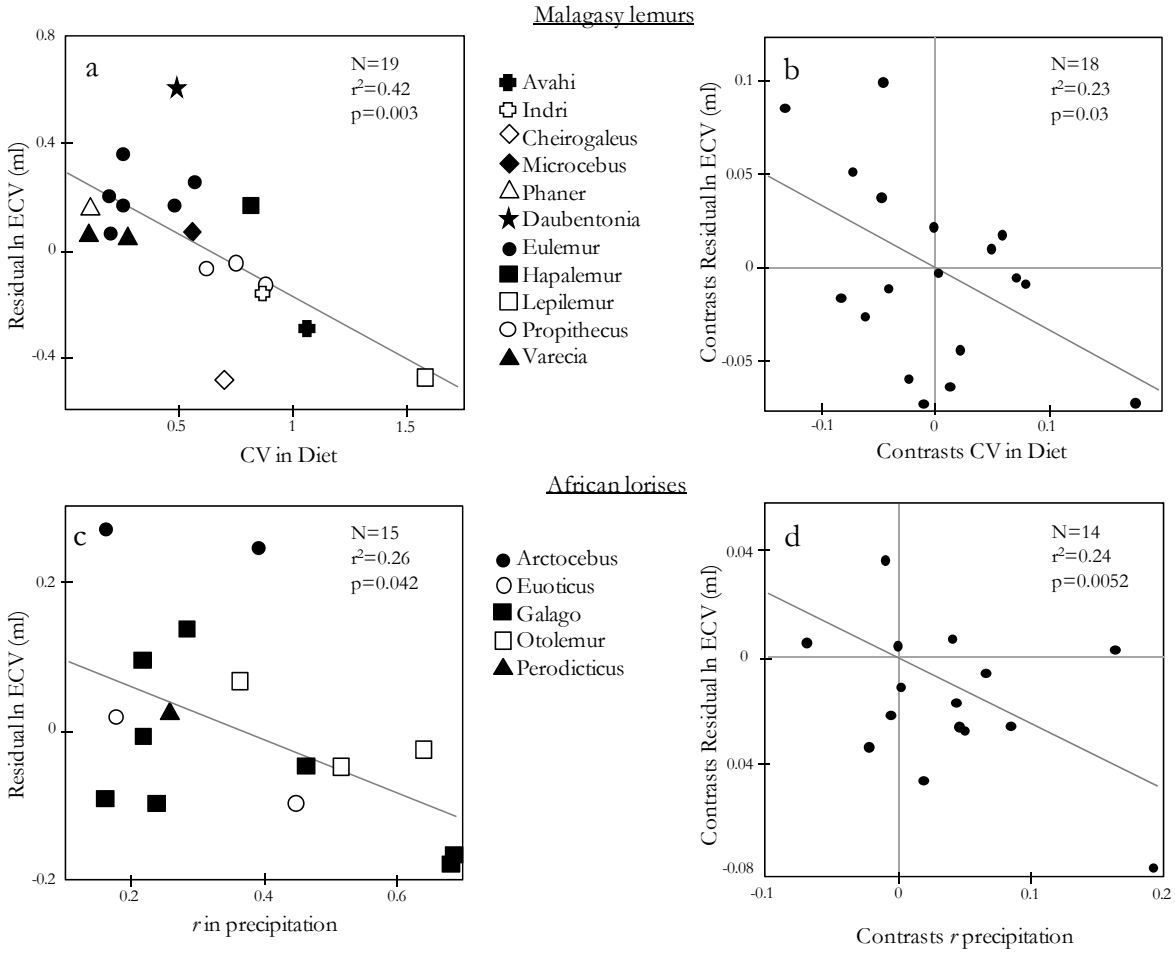

Figure 2.2. Correlation between brain size and experienced seasonality (CV in diet) of lemurs in (a) the species values and (b) independent contrasts, and the correlation between brain size and precipitation seasonality (*r* in precipitation) of lorises in (c) the species values and (d) in dependent contrasts. In both taxa experienced seasonality shows a significant negative influence on brain size.

Discussion

In both Malagasy lemurs and African lorises, we found that species experiencing pronounced seasonal changes in food availability have relatively smaller brains, controlling for possibly confounding variables such as body mass, phylogenetic relatedness, diet and specialized adaptations. For the lemurs, experienced seasonality as proxied by variation in intake of preferred food was more strongly correlated with brain size than were either plant productivity or climatic seasonality, indicating the occurrence of buffer effects. In the African lorises, on the other hand, we assume that climatic seasonality aptly reflects the conditions experienced by the animals due to the dietary and behavioral homogeneity of this group. Although we were not able to test this assumption due to the lack of detailed data on diet in this group, the negative relationship we found between relative brain size and climatic seasonality lends support to our expectation. In contrast to lemurs, plant productivity is not relevant in lorises, as availability of their most important diet component, insects, is influenced more by rainfall than by leaf production (Wolda 1978; Coley and Barone 1996). This discrepancy between rainfall and leaf production can arise when plant productivity is limited by irradiance, not rainfall, as is the case in Central Africa (Wright and van Schaik 1994). Thus, the observed negative correlation between rainfall seasonality and brain size in African lorises supports our predictions.

Our results therefore unequivocally support the energetic view of brain size evolution proposed by among others Aiello and Wheeler (1995) and Martin (1996). Recently, Isler and van Schaik (Isler and van Schaik 2006b, 2009a) emphasized the utility of a broad theoretical framework to examine the energetic aspects of brain size evolution, which allows specific predictions to be tested. Many of these have already been confirmed (Isler and van Schaik 2006a; Isler and van Schaik 2006b, 2009b). Accordingly, several authors now stress the importance of considering energetic constraints (e.g. Dunbar 2009), which have nonetheless rarely been considered in predictions or tests of cognitive buffer effects. In the present study we show that ecological conditions are correlated with encephalization in strepsirrhine primates. As predicted, recurring periods of food scarcity evolutionarily constrain brain size because net energy availability is reduced during these times. In more seasonal habitats, primates evolved strategies that allow them to expend less energy to compensate for the reduction in energy intake, such as reproducing seasonally (assuming the reproductive cycle can be completed in less than a year), switching to energetically less valuable, but widely available, fallback foods, or even entering

torpor or hibernation during the lean periods. Nevertheless, our results show that such physiological buffers do not sufficiently compensate for reduced energy availability to provide equal opportunities to enlarge brain size as compared to species living in less variable habitats. Moreover, our within-genus comparison within the lemurs provides evidence that these constraints can work in a relatively short time (1-7 Mya).

The negative correlation between brain size and habitat seasonality would be even stronger if larger brains would not also have some benefit. A cognitive buffer would allow species to dampen the fluctuations in the supply of preferred foods and thus limit fluctuations in their energy intake to a lower level than expected, by finding or accessing hidden or protected food sources (e.g. extractive foraging) or by switching to other microhabitats. In this case, seasonality of the habitat might act as a positive selection pressure for a relatively large brain that would counteract the effect of energy constraints. One might therefore expect a positive correlation between brain size and the difference between habitat seasonality and experienced seasonality, i.e. temporal variation in dietary energy content (Figure 2.1b). The weakness of the correlation found in this study may be explained by various shortcomings of the dataset. In combination with a relatively small sample, the studies of diet composition may be too heterogeneous depending on observation protocols and characteristics of the study sites. The resulting error could weaken the correlations if phylogenetic methods are used (Martin et al. 2005). On the other hand, the weak result could simply reflect the fact that a cognitive buffer effect is rare within lemurs, as almost all species experience a high degree of perceived habitat seasonality. The only obvious exception is the aye-aye (*Daubentonia madagascariensis*), the single extant member of a family that split off from the rest of the lemurs at least 60 million years ago (phylogenetic relations are debated, see Martin 2000). This peculiar primate's brain is exceptionally large, within the range of anthropoid primates, and is matched by a relatively high basal metabolic rate for a lemur (Isler et al. 2008; Barrickman and Lin 2010). Aligning these two characteristics, the experienced seasonality of the aye-aye seems to be low; as an extractive forager its diet consists of high quality food sources throughout the year (Sterling 1994) and it is the only lemur that does not have a breeding season (Beattie et al. 1992; Sterling 1994). Thus extractive foraging is apparently acting as a cognitive buffer in the aye-aye.

It would be interesting to expand our study to the extinct lemurs that were mostly larger in body mass and may have shown extreme life history characteristics exceeding the range of extant species (Catlett et al. 2010). The presumably most folivorous taxon, *Megaladapis*, has the

relatively smallest brain, and the giant lemur thought to have a similar diet as the aye-aye, *Archaeolemur*, has the relatively largest brain (Godfrey et al. 2004; Schwartz et al. 2005). Assessing the degree of experienced seasonality is difficult for extinct species, but current reconstructions of diet and lifestyle for those species with known brain size are in accordance with our findings. The two species with the relatively largest brains (*Archaeolemur* and *Hadropithecus*) are those for which the assumption of a non-seasonal breeding pattern seems most appropriate (Catlett et al. 2010). Interestingly, these authors found that (large) brain size is a better predictor of (low) reproductive rates than is body mass, independently confirming a more general trend found in eutherian mammals (Isler and van Schaik 2009a). More detailed studies on the relationships between ecological adaptations, life history traits and brain size are warranted in the extinct lemur species.

The groups analyzed in this study were small to medium-sized primates and relatively small-brained compared to anthropoid primates, but still relatively large-brained compared to other mammals of similar body size. Therefore, both Malagasy lemurs and African lorises use a relatively large percentage of their basal metabolism to maintain their brains, and can therefore be expected to experience stronger energetic constraints on brain size than for instance cercopithecoid monkeys. The within-genus comparison among the lemurs also showed a stronger effect within the smaller sister taxa (*Microcebus, Cheirogaleus*) than the larger ones (*Propithecus*). It remains to be seen whether the negative correlation between perceived seasonality and brain size also exists in large-bodied primates, or whether cognitive buffer effects will be stronger.

In conclusion, this study of strepsirrhine primates supports the argument that seasonality has acted primarily as a constraint rather than a positive selective pressure on brain size. We propose that the effect of seasonality on strepsirrhine brain sizes and the reduced brain size of island dwarfs are special cases of a far more general phenomenon. In general, conditions under which animals are forced to deal with periods of unavoidable food shortage, as a result of seasonality (this study), living on islands (Köhler and Moyà-Solà 2004; Weston and Lister 2009), and El Niño droughts (Taylor and van Schaik 2007), should lead to relatively smaller brains.

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Appendix Chapter 2

Table A2.1. PGLS analyses on multivariate regressions between seasonality and brain size, controlling for body mass in both lemurs and lorises and group size in lemurs using different tree phylogenies.

	Tree 1 (based on Horvath et al. 2008 [1])			**Tree 2 (based on Arnold et al. 2010 [2])**			**Tree 3 (based on Bininda-Emonds et al. 2007[3])**			**Tree 4 (based on Orlando et al. 2008[4])**		
Seasonality measure	t-ratio	*P*	λ	t-ratio	*P*	λ	t-ratio	*P*	λ	t-ratio	*P*	λ
CV in diet for lemurs (N=19)	-3.35	0.0043	1.00	-3.39	0.0041	1.00	-3.46	0.0035	1.00	-3.11	0.0072	1.00
r in precipitation for lorises (N=16)				-2.95	0.0113	0.98	-2.88	0.0128	0.97			

Note: In the trees from Horvath et al. (2008) and Orlando et al. (2008), loris phylogeny was not included. The negative correlation between seasonality and relative brain size remains unaffected by the type of phylogeny that is used. All λ values are not significantly different from 1. CV = coefficient of variation.

Table A2.2. Bivariate analyses comparing relative brain sizes between lemur sister taxa inhabiting either the less seasonal eastern or more seasonal western side of Madagascar, based on individual ECV measurements from known locations.

Sister taxa in Genus	**Body mass Range (g)**	**N**	***P***	**Relative brain size, West vs East**
Microcebus (*rufus* vs *murinus*)	40-60	21 (8 vs 13)	<0.0001	West < east
Cheirogaleus (*major* vs *medius*)	100-500	45 (12 vs 33)	<0.0001	West < east
Lepilemur (*mustelinus* vs *ruficaudatus*)	700-1,000	53 (33 vs 20)	<0.0001	West < east
Eulemur (*albifrons, rubriventer, fulvus* vs *mongoz, rufus*)	1,200-2,100	23 (8 vs 15)	0.0003	West < east
Propithecus (*diadema, edwardsi* vs *coquereli, deckenii, verreauxi)*	3,200-6,500	40 (13 vs 27)	0.5515	West = east

Note: Species-specific body mass data are listed in Table A4. In all taxa except the *Propithecus* spp., the western sister species have relatively smaller brains than the eastern sister species.

Table A2.3. Bivariate correlations (phylogenetic generalized least squares) between the seasonality measures and brain size in Malagasy lemurs and African lorises, controlling only for body mass.

	Malagasy lemurs (climate: N= 36; diet: N=19)			**African lorises (N=16)**		
Covariable with body mass vs. brain size	t- ratio	*P*	λ	t-ratio	*P*	λ
CV in diet	-2.12	0.049	1.00			
CV in plant productivity	-2.34	0.026	0.97	-0.32	0.757	0.72
r in precipitation	-0.89	0.382	0.96	-2.94	0.011	0.98
CV in precipitation	-0.85	0.404	0.96	-2.19	0.047	1.00
P2T	1.79	0.083	0.98	2.03	0.062	1.00
SD in temperature	-0.72	0.480	0.96	-2.65	0.020	1.00

Note: All λ values are not significantly different from 1. CV = coefficient of variation. P2T = number of dry months.

Table A2.4. List of species and data used for this study.

Species	BoM[†] (g)	ECV (ml)[‡]	N ECV[‡]	Res ln ECV[‡]	P2T	CV in prec.	*r* in prec.	SD in temp.	CV in NDVI	CV in Diet[†]	% leaves	Study Site[§]	Group size.[*]	Diur.[¶]	Hib.[**]
Avahi laniger	1032 [5]	9.64	19	-0.252	11.1	61.4	0.390	23.0	10.2				5	2	No
Avahi occidentalis	801 [6]	7.92	2	-0.315	6.0	118.0	0.758	13.0	19.0	1.05 [7]	89.9	Ampijoroa	5	2	No
Cheirogaleus major	356 [8]	5.51	7	-0.040	11.9	51.3	0.325	21.5	9.1					2	Yes
Cheirogaleus medius	139 [9-11]	2.53	19	-0.235	4.9	129.4	0.778	23.1	20.9	0.69 [9]	4.0	Kirindy	5	2	Yes
Cheirogaleus ravus	468˚	6.00	1	-0.154	12.0	45.0	0.294	21.8	10.0					2	Yes
Daubentonia madagascariensis	2800 [12]	46.06	5	0.566	9.2	74.2	0.480	18.2	11.4	0.49 [13]	0.0	Nosy Mangabe	2	2	No
Eulemur albifrons	1811˚	23.10	23	0.181	9.5	57.4	0.370	20.4	7.4	0.19 [14]	14.3	Andranobe, Masoala Nat. Park	11	1	No
Eulemur collaris	1660˚	23.11	8	0.278	11.1	63.5	0.409	22.5	5.3					1	No
Eulemur coronatus	1422˚	19.17	8	0.203	7.0	90.9	0.599	18.4	8.3				6	1	No
Eulemur fulvus	2300[¥]	24.78	18	0.090	9.4	73.9	0.477	22.9	10.9	0.26 [15, 16]	24.6	Ampijaroa, Mayotte	18	1	No
Eulemur macaco	1908˚	22.65	8	0.129	6.8	91.6	0.604	13.8	13.1	0.47 [17]	44.7	Lokobe	10	1	No
Eulemur mongoz	1212[¥]	17.46	13	0.188	6.5	97.9	0.630	13.8	16.9	0.57 [15]	36.4	Ampijaroa	4	1	No
Eulemur rubriventer	2067[5]	24.29	19	0.144	9.8	80.2	0.515	20.7	11.7	0.25 [18]	18.5	Ranomafana	5	1	No

Eulemur rufus	2154 [5, 19]	22.20	25	0.020	4.2	121.8	0.745	21.5	19.0	0.20 [18]	22.0	Ranomafana	18	1	No
Hapalemur alaotrensis	1239 [20-22]	13.80	1	-0.026	5.0	106.0	0.695	23.3	14.0					0	No
Hapalemur griseus	935 [5, 22]	13.74	36	0.127	10.6	60.1	0.386	21.2	9.1	0.81 [23]	100.0	Ranomafana	6	0	No
Hapalemur occidentalis	802˚	13.75	2	0.285	7.0	102.0	0.673	15.1	11.5					0	No
Indri indri	5830 [24]	34.81	37	-0.220	11.7	63.5	0.409	22.1	8.1	0.87 [24-26]	68.6	Analamazoatra, Mantadia, Betampona	6	0	No
Lemur catta	2210 [27]	23.41	7	0.084	5.0	84.3	0.520	27.9	18.0				30	0	No
Lepilemur dorsalis	817 [28]	6.50	3	-0.477	8.0	90.0	0.599	12.9	27.0					2	No
Lepilemur edwardsi	915 [29]	7.24	4	-0.500	6.0	113.5	0.729	17.3	24.0	1.58 [7]	81.1	Ampijoroa	3	2	No
Lepilemur microdon	1178˚	8.17	3	-0.514	12.0	58.3	0.373	22.9	8.3				2	2	No
Lepilemur mustelinus	712 [28, 30]	9.56	5	0.008	12.0	63.4	0.396	24.1	7.0					2	No
Lepilemur ruficaudatus	725 [30, 31]	7.56	14	-0.240	4.2	135.4	0.800	25.0	19.6					2	No
Microcebus murinus	59 [32-36]	1.54	27	-0.015	5.8	62.4	0.380	29.1	12.0				5	2	Yes
Microcebus rufus	46 [8, 32, 37]	1.65	21	0.104	9.6	65.8	0.420	22.3	10.4	0.57 [38]	0.0	Ranomafana	4	2	Yes
Mirza coquereli	311 [39]	5.35	2	0.026	5.0	120.0	0.734	19.1	13.5					2	Yes
Phaner furcifer	327 [40]	6.75	2	0.145	11.5	51.0	0.326	17.8	10.0	0.10 [40]	0.0	Kirindy	4	2	No
Phaner pallescens	327	6.59	3	0.199	3.3	112.7	0.702	26.9	24.3					2	No

Propithecus coquereli	3672[¥] [41]	30.00	5	-0.036	5.4	123.4	0.777	14.9	14.4					0	No
Propithecus deckenii	3430[¥]	27.76	16	-0.064	5.9	119.1	0.760	14.7	16.1					0	No
Propithecus diadema	6500 [24]	38.47	14	-0.195	9.0	68.6	0.449	21.5	10.0	0.87 [15, 42]	48.1	Mantadia, Tsinjoarivo	9	0	No
Propithecus edwardsi	5656 [5]	37.34	4	-0.127	8.5	81.0	0.524	24.3	12.5	0.62 [43]	47.3	Ranomafana	10	0	No
Propithecus verreauxi	3250 [41]	26.05	28	-0.099	4.4	97.4	0.612	24.9	20.9	0.74 [44]	53.3	Ampijaroa, Kirindy	12	0	No
Varecia rubra	3300 [45]	29.37	8	0.006	12.0	43.0	0.284	20.5	5.3	0.10 [14]	11.8	Andranobe, Masoala Nat. Park	16	0	No
Varecia variegata	3600 [46, 47]	30.88	23	-0.007	10.2	64.0	0.415	21.8	9.5	0.26 [47]	8.6	Nosy Mangabe	16	0	No
Arctocebus aureus	200 [48]	5.89	2	0.260	9.5	55.5	0.163	6.9	20.5				2	2	No
Arctocebus calabarensis	309 [49]	7.41	12	0.237	9.5	61.8	0.395	8.5	20.2				2	2	No
Euoticus elegantulus	274	5.55	11	0.017	10.7	57.7	0.174	7.7	22.3				7	2	No
Euoticus pallidus	300	5.19	9	-0.103	10.2	67.2	0.448	8.4	20.9					2	No
Galago alleni	260	5.78	5	0.089	10.0	58.4	0.214	7.2	29.6				4	2	No
Galago demidoff	61	2.62	49	0.132	9.8	53.5	0.279	7.7	19.1				5	2	No
Galago gallarum	200	4.32	5	-0.051	8.4	99.6	0.464	11.4	23.0					2	No
Galago matschiei	210	4.62	4	-0.013	11.0	40.8	0.218	4.1	12.0					2	No
Galago moholi	190	3.66	62	-0.187	4.6	100.9	0.685	34.8	21.5				3	2	No
Galago senegalensis	213	3.95	193	-0.176	5.4	108.5	0.688	20.0	31.7					2	No

Galago thomasi	116	3.01	3	-0.100	11.7	33.7	0.159	2.8	10.3					2	No
Galago zanzibaricus	143	3.36	7	-0.107	8.4	62.4	0.241	15.3	15.1				6	2	No
Otolemur crassicaudatus	1150	11.84	27	-0.053	6.7	81.3	0.518	20.3	19.3				6	2	No
Otolemur garnettii	764	10.49	15	0.062	6.1	80.7	0.362	14.1	12.5					2	No
Perodicticus potto	1172	12.87	26	0.020	10.3	53.4	0.258	7.4	18.9				2	2	No

Notes: ECV = endocranial volume; *N* ECV = sample size of ECVs; Res = residual ECVs (ECV relative to body mass); P2T = number of dry months; prec. = precipitation; temp. = temperature; CV = coefficient of variation; and NDVI = normalized difference vegetation index.

[†]References are between brackets, unless stated otherwise body mass was taken from Smith and Jungers (1997).

[˚]Estimated body mass from bizygomatic breadth of the same skull from which ECV was measured.

[‡]Males and females averaged together.

[§]Study site from where dietary information was collected.

[*]Maximum group size according to Rowe (1996).

[¶]Diurnality, 0 = diurnal, 1 = cathemeral, 2 = nocturnal.

[**]Species that show hibernation or torpor during some parts of the year.

[¥]Pastorini, personal communication.

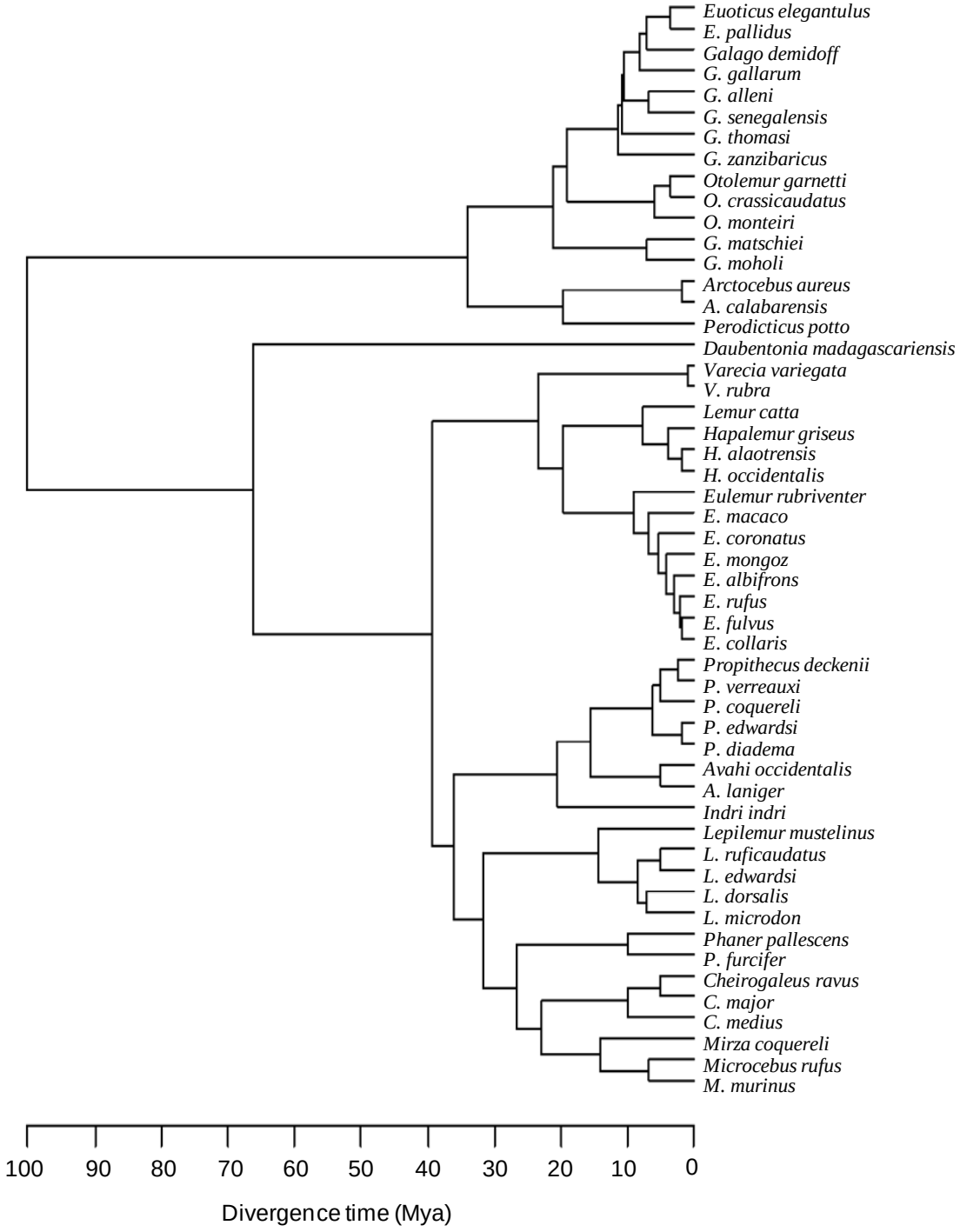

Figure A2.1. This phylogeny was used for the analyses reported in the main text, based on Horvath et al. 2008 and supplemented with data from the 10K ConsensusTree (Arnold et al. 2010).

References appendix Chapter 2

1. Horvath, J. E., D.W.Weisrock, S. L. Embry, I. Fiorentino, J. P. Balhoff, P. Kappeler, G. A. Wray, et al. 2008. Development and application of a phylogenomic toolkit: Resolving the evolutionary history of Madagascar's lemurs. Genome Research 18(3): p. 489-499.
2. Arnold, C., L.J. Matthews, and C.L. Nunn. 2010. The 10kTrees website: a new online resource for primate phylogeny. Evolutionary Anthropology 19:114–118.
3. Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, et al. 2007. The delayed rise of present-day mammals. Nature 446:507–512.
4. Orlando, L., S. Calvignac, C. Schnebelen, C. J. Douady, L. R. Godfrey, and C. Hanni. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. BMC Evolutionary Biology 8: p 121–130
5. Glander, K. E., P. C. Wright, P. S. Daniels, and A. M. Merenlender. 1992. Morphometrics and Testicle Size of Rain-Forest Lemur Species from Southeastern Madagascar. Journal of Human Evolution 22(1): p. 1-17.
6. Thalmann, U. and T. Geissmann. 2000. Distribution and geographic variation in the western woolly lemur (*Avahi occidentalis*) with description of a new species (*A. unicolor*). International Journal of Primatology 21(6): p. 915-941.
7. Thalmann, U. 2001. Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. International Journal of Primatology 22(2): p. 287-324.
8. Wright, P.C. and L.B. Martin. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar, *in* Creatures of the Dark, L. Alterman, G. A. Doyle and M. K. Izard, Editors. Plenum, New York. P. 45-60.
9. Fietz, J. and J.U. Ganzhorn. 1999. Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? Oecologia 121(2): p. 157-164.
10. Hladik, C.M., P. Charles-Dominique, and J.J. Petter. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar, *in* Nocturnal Malagasy primates: ecology, physiology and behavior, C. M. Hladik, P. Charles-Dominique and J.J. Petter, Editors. Academic Press: New York. P. 41-73.
11. Muller, A.E. 1999. Aspects of social life in the fat-tailed dwarf lemur (*Cheirogaleus medius*): Inferences from body weights and trapping data. American Journal of Primatology 49(3): p. 265-280.

12. Sterling, E. 1994. Taxonomy and Distribution of *Daubentonia* – a Historical-Perspective. Folia Primatologica 62(1-3): p. 8-13.
13. Sterling, E. 1993 Behavioral ecology of the aye-aye (*Daubentonia Madagascariensis*) on Nosy Mangabe, Madagascar. PhD Dissertation. Yale University: New Haven, CT
14. Vasey, N. 2004. Circadian rhythms in diet and habitat use in red ruffed lemurs (*Varecia rubra*) and white-fronted brown lemurs (*Eulemur fulvus albifrons*). American Journal of Physical Anthropology 124(4): p. 353-363.
15. Rasmussen, M.A. 1999. Ecological Influences on Activity Cycle in Two Cathemeral Primates, the Mongoose Lemur (*Eulemur mongoz*) and the Common Brown Lemur (*Eulemur fulvus fulvus*). PhD Dissertation. Duke University: Durham.
16. Tarnaud, L. 2006. Feeding behavior of lactating brown lemur females (*Eulemur fulvus*) in 37omate37: Influence of infant age and plant phenology. American Journal of Primatology 68(10): p. 966-977.
17. Andrews, J.R. and C.R. Birkinshaw. 1998. A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, *Eulemur macaco* (Primates : Lemuridae), in Lokobe forest, Madagascar. Folia Primatologica 69: p. 175-182.
18. Overdorff, D.J. 1993. Similarities, Differences, and Seasonal Patterns in the Diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. International Journal of Primatology 14(5): p. 721-753.
19. Johnson, S. E., A. D. Gordon, R. M. Stumpf, D. J. Overdorff, and P. C. Wright. 2005. Morphological variation in populations of *Eulemur albocollaris* and *E. fulvus rufus*. International Journal of Primatology 26(6): p. 1399-1416.
20. Mutschler, T., A.T.C. Feistner, and C.M. Nievergelt. 1998. Preliminary field data on group size, diet and activity in the Alaotran gentle lemur *Hapalemur griseus alaotrensis*. Folia Primatologica 69(5): p. 325-330.
21. Mutschler, T., C.M. Nievergelt, and A.T.C. Feistner. 2005. Social organization of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). American Journal of Primatology 50(1): p. 9-24.
22. Tan, C.L. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. International Journal of Primatology 20(4): p. 547-566.
23. Overdorff, D.J., S.G. Strait, and A. Telo. 1997. Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in Southeastern Madagascar. American Journal of Primatology 43(3): p. 211-223.

24. Powzyk, J.A. 1997. The socio-ecology of two sympatric indrids, *Propithecus diadema diadema* and *Indri indri*: A comparison of feeding strategies and their possible repercussions on species-specific behaviors. PhD Dissertation. Duke University: Durham.
25. Britt, A., N. J. Randriamandratonirina, K. D. Glasscock, and B. R. Iambana. 2002. Diet and feeding 38omate38r of *Indri indri* in a low altitude rain forest. Folia Primatologica 73(5): p. 225-239.
26. Pollock, J.I. 1977. The ecology and sociology of feeding in *Indri indri*, *in* Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes, T. Clutton-Brock, Editor. Academic Press: London. P. 37-69.
27. Sussman, R.W. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza-Mahafaly Reserve, Madagascar. American Journal of Physical Anthropology 84(1): p. 43-58.
28. Andriaholinirina, N., J. Fausser, C. Roos, D. Zinner, U. Thalmann, C. Rabarivola, I. Ravoarimanana, et al. 2006. Molecular phylogeny and taxonomic revision of the sportive lemurs (Lepilemur, Primates). Bmc Evolutionary Biology 6: p. 17 -30.
29. Kappeler, P.M. 1997. Intrasexual selection and testis size in strepsirhine primates. Behavioral Ecology 8(1): p. 10-19.
30. Ganzhorn, J.U.2002. Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. Oecologia 131(3): p. 427-435.
31. Schmid, J. and J.U. Ganzhorn. 1996. Resting metabolic rates of *Lepilemur ruficaudatus*. American Journal of Primatology 38(2): p. 169-174.
32. Atsalis, S. 1999. Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. International Journal of Primatology 20(6): p. 883-910.
33. Jolly, A. 1984. The puzzle of female feeding priority, *in* Female Primates: Studies by Woman Primatologists, M.F. Small, Editor. Alan R. Liss: New York. P. 197–215.
34. Fietz, J. 1998. Body mass in wild *Microcebus murinus* over the dry season. Folia Primatologica 69: p. 183-190.
35. Rasoloarison, R.M., S.M. Goodman, and J.U. Ganzhorn. 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. International Journal of Primatology 21(6): p. 963-1019.
36. Schmid, J. and P.M. Kappeler. 1994. Sympatric mouse lemurs (*Microcebus spp.*) in Western Madagascar. Folia Primatologica 63(3): p. 162-170.
37. Atsalis, S., J. Schmid, and P.M. Kappeler. 1996. Metrical comparisons of three species of mouse lemur. Journal of Human Evolution 31(1): p. 61-68.

38. Atsalis, S. 1999. Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. International Journal of Primatology 20(2): p. 193-229.
39. Kappeler, P.M., R. M. Rasoloarison, L. Razafimanantsoa, L. Walter, and C. Roos. 2005. Morphology, behavior and molecular evolution of giant mouse lemurs (*Mirza spp.*) Gray, 1870, with description of a new species. Primate Report 71: p. 3 –26.
40. Schülke, O. 2003. To breed or not to breed – food competition and other factors involved in female breeding decisions in the pair-living nocturnal fork-marked lemur (*Phaner furcifer*). Behavioral Ecology and Sociobiology 55(1): p. 11-21.
41. Ravosa, M.J., D.M. Meyers, and K.E. Glander. 1993. Relative Growth of the Limbs and Trunk in Sifakas – Heterochronic, Ecological, and Functional Considerations. American Journal of Physical Anthropology 92(4): p. 499-520.
42. Irwin, M.T. 2008. Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. International Journal of Primatology 29(1): p. 95-115.
43. Hemingway, C.A. and N. Bynum. 2005. The Influence of Seasonality on Primate Diet and Ranging, *in* Seasonality in Primates, D.A. Brockman and C.P. van Schaik, Editors. Cambridge University Press: New York. P. 57-104.
44. Richard, A.F. 1978. Behavioral variation: Case study of a Malagasy lemur. Lewisburg: Bucknell University Press.
45. Vasey, N. 2003. *Varecia*, ruffed lemurs, *in* The Natural History of Madagascar, S.M. Goodman and J.P. Benstead, Editors. University of Chicago Press: Chicago. P. 1332–1336.
46. Balko, E.A. 1998. A Behaviorally Plastic Response to Forest Composition and Logging Disturbance by *Varecia variegate variegata* in Ranomafana National Park, Madagascar. PhD Dissertation. State University of New York: New York.
47. Morland, H.S. 1991. Social organization and ecology of black and white ruffed lemurs (*Varecia variegate variegata*) in lowland rain forest, Nosy Mangabe, Madagascar. PhD Dissertation. Yale University: New Haven, CT.
48. Charles-Dominique, P. 1997. Ecology and Behaviour of Nocturnal Prosimians. London: Duckworth.
49. Jewell, P.A. and J.F. Oates. 1969. Ecological observations on the Lorisoid primates of African lowland forests. Zoologica Africana 4(2): p. 231-248.
50. Smith, R.J. and W.L. Jungers. 1997. Body mass in comparative primatology. Journal of Human Evolution 32(6): p. 523-559.
51. Rowe, N. 1996. The pictorial guide to the living primates. New York: Pogonias Press.

Chapter 3.

Large Brains Buffer Energetic Effects of Seasonal Habitats in Catarrhine Primates

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Abstract

Ecological factors have been shown to be important for brain size evolution. In this comparative study among catarrhine primates, we examine two different ways in which seasonality may be related to brain size. First, seasonality may impose energetic constraints on the brain because it forces animals to deal with periods of food scarcity (Expensive Brain hypothesis). Second, seasonality may act as a selective pressure to increase brain size, as behavioral flexibility helps to overcome periods of food scarcity (Cognitive Buffer hypothesis). Controlling for phylogeny, we found a strong negative relationship between brain size (relative to body mass) and the degree of experienced seasonality, as estimated by the variation in net energy intake. However, we also found a significant positive relationship between relative brain size and the effect of so-called cognitive buffering, proxied by the difference between environmental seasonality and the seasonality in net energy intake actually experienced by the animals. These results show that both energetic constraints of seasonal habitats as well as cognitive buffering affect brain size evolution, leaving environmental seasonality uncorrelated to brain size. With this study we show the importance of simultaneously considering both costs and benefits in models of brain size evolution.

Introduction

To explain the observed variation in primate brain sizes, several adaptive hypotheses have been proposed (reviewed in Healy and Rowe 2007). Most of these hypotheses have focused on relating the evolution of brain size to the selective benefits due to enhanced cognitive abilities (e.g. Dunbar 1998; Tomasello 1999; Deaner et al. 2007; Reader et al. 2011) which may be favored by certain ecological conditions (Reader and Laland 2002; Fish and Lockwood 2003; Shultz and Dunbar 2006). However, environmental conditions may also constrain the evolution of relatively large brains. In recent years, we have followed an approach of addressing brain size evolution from a purely energetic perspective, that is, applying the Expensive Brain Framework (Isler and van Schaik 2009a). Brain tissue requires a high and continuous energy supply (Mink et al. 1981) and consequently serious starvation, especially during development, leads to permanent brain damage (Lukas and Campbell 2000). The costs of brain function cannot be temporarily reduced (except probably in deeply hibernating rodents, Krilowicz et al. 1988). Evolution of an increased brain size (relative to body size) is therefore only possible if either total energy throughput is increased, the energy allocation to other functions is reduced, or a combination of the two is achieved (see also Martin 1981; Aiello and Wheeler 1995; Isler and van Schaik 2009a). This energetic perspective predicts that brain size is reduced where animals experience periodic energy shortages in a seasonal habitat. Even if physiological buffers such as fallback foods, fat storage, reduced activity, or hibernation allow for survival during lean periods, the net energy availability is still reduced relative to the season in which food is abundant, and brains are expected to be relatively smaller in comparison with a similar species that does not experience such seasonal food shortages.

Therefore, the central prediction of the Expensive Brain Framework is that, *ceteris paribus*, a species' brain size is negatively related to the intensity of seasonality in net food intake, i.e. the "experienced seasonality" (XPR, Figure 3.1a). Recently, we confirmed this prediction in African strepsirrhine primates (van Woerden et al. 2010). Additional support comes from a comparison of orangutans subspecies (Taylor and van Schaik 2007) and studies in various mammals showing that the dwarfing effects of unavoidable food scarcity on brain size exceed those on body size on small oceanic islands (Filin and Ziv 2004; Lomolino 2005; Korstjens et al. 2007; Niven 2007; Weston and Lister 2009).

Environmental seasonality does not lead to seasonality in food intake, if the decrease in food availability is fully compensated by an increase in foraging effort or a switch to other (hidden) high-quality food sources. The Cognitive Buffer hypothesis (see Allmann et al. 1993; Deaner et al. 2003; Sol 2009) predicts that larger brains provide the cognitive abilities that allow for increased behavioral flexibility, which among other things, facilitates the buffering of environmental seasonality. Thus larger brained species are supposed to outperform smaller brained species in more seasonal habitats, which are more cognitively demanding because preferred food sources are more difficult to (re)locate in space or time (Klopfer and MacArthur 1960; Sol et al. 2005a; Sol et al. 2008). According to this hypothesis, selection is expected to favor species with relatively large brains in more seasonal habitats. Support comes mainly from studies in birds. Schuck-Paim et al. (2008) found a positive correlation between climatic variability and brain size in Neotropical parrots. In addition, migrating bird species have smaller brains than non-migrating bird species (Winkler et al. 2004; Sol et al. 2005b), which can be reflecting a cognitive buffer effect in the residential species (Sol et al. 2005b) or a reduced selective advantage of enhanced cognitive performance in migratory species (Sol et al. 2010). In contrast, evidence of cognitive buffer effects in mammals is very limited (Sol et al. 2008). Reader and MacDonald (2003) reported that innovation rate or neocortex ratio (both closely related with overall brain size) are not correlated with climatic variability among African primates.

However, cognitive buffering and energetic constraints on brain size are not mutually exclusive. Indeed, we expect that cognitive buffering may only partially reduce the experienced seasonality of a species, still leaving the nonbuffered remnant of environmental seasonality to constrain brain size. To investigate the cognitive buffer effect, we must therefore not merely consider the environmental seasonality, but also the amount of buffering, that is, the difference between food availability and energy intake. Here, we assess the temporal variation in net energy intake, a measure of experienced seasonality (XPR) by the monthly variation in consumption of major diet components (fruits, flowers, young and mature leaves and insects) multiplied by their quality (as in van Woerden et al. 2010). If energetic constraints on brain size apply, we expect a negative correlation between brain size and this experienced seasonality. If cognitive buffering takes place to cope with harsh environmental conditions, the experienced seasonality is smaller than the variation in food availability, which is proxied by the seasonality of the environment (ENV). Animals that cognitively buffer will manage to keep their energy intake relatively constant despite dramatic environmental fluctuations. Therefore, the *difference* between the

environmental (i.e. expected) seasonality and the seasonality that is experienced (ENV-XPR) tells us how much buffering is taking place. The Cognitive Buffer hypothesis then predicts brain size to be positively related to the amount of buffering (Figure 3.1b).

Our recent study in Malagasy lemurs (van Woerden et al. 2010) was the first to look at both energetic constraints and cognitive buffering effects of seasonality on brain size evolution using this approach and found strong support for energetic constraints, but only a weak indication for a cognitive buffer effect. In the present study, we investigate whether cognitive buffering is more important in the catarrhine clade of nonhuman primates, consisting of Old World monkeys and apes. Catarrhine primates have greater cognitive abilities (reviewed in Fichtel and Kappeler 2010) and are generally larger-brained relative to body mass than lemurs (Isler et al. 2008). We test (1) the predictions of the Expensive Brain framework by examining the relationship between experienced seasonality (XPR) and brain size, (2) the predictions of the Cognitive Buffer hypothesis by looking at the relationship between the amount of buffering (ENV-XPR) and brain size, and (3) whether one of these effects prevails by looking at the relationship between environmental seasonality and brain size.

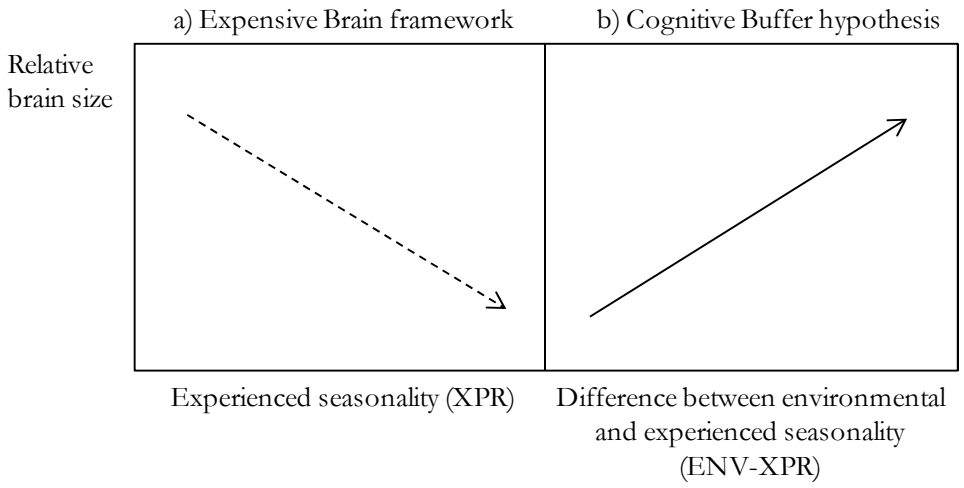

Figure 3.1. The two hypotheses presented in this paper with their predicted relationship between seasonality and brain size. Note that each hypothesis forms a prediction between relative brain size and a different, nonexclusive measure of seasonality.

Methods

Brain and body size

Our sample includes only female wild adult specimens (third molar present) of which the original provenance was known, in order to exclude a possible effect of captivity and a bias through sexual dimorphism (Plavcan and van Schaik 1992; Smith and Cheverud 2002). Female brain size of 70 species of nonhuman catarrhine primates were assessed through measuring endocranial volumes (ECV) using glass beads in eight European and four American museums and added to the dataset of Isler et al. (2008) to yield a total of 1756 female skulls, 1576 of which with known origin from 1229 different locations. Conversion to brain mass is not needed as the two have been shown to correlate isometrically in primates (Isler et al. 2008). Because it has been documented that primates tend to have smaller body sizes in more seasonal habitats (Albrecht et al. 1990; Lehman et al. 2005; Plavcan et al. 2005), it is important to include body size as a covariate in the analyses. Female body masses from wild study populations were collected from literature sources, or if possible taken from the same museum specimens that ECV was measured from (Table A3.1). Species were included if more than five measurements were available to calculate an average female ECV value (Table A3.1).

Seasonality

Experienced seasonality (XPR)

We measured experienced seasonality by using temporal variation in the time spent feeding on diet components (and thus their estimated consumption) weighted for their nutritional value. Monthly dietary data were collected by literature research. Only studies that reported consumption of different dietary items over 12 consecutive months were included. In total, dietary data were available for 63 populations of 36 catarrhine species (Table A3.1). The coefficient of variation (CV) in consumption of dietary components over a year was estimated as follows. From the monthly means of the time spent feeding on the following food items (insects, fruit/seeds, flowers, young leaves and mature leaves), we calculated the energy gained per month by multiplying the sum of each item by its energetic quality (eight for insects, five for fruits, seeds and flowers, three for young leaves and one for mature leaves, as calculated from gram crude fiber per kilogram of dry matter by Langer 2003). Fiber content is commonly used as a measure of digestibility and thus energy gained per unit time (McNab 2002). The coefficient of

variation (CV) among months in this measure yielded the CV of net energy intake. The standard deviation (SD) in this measure was larger between species (0.07) than between populations (0.04), demonstrating that the variation is mostly between species. We assumed an equal energy expenditure throughout the year, because the variation of energy expenditure of wild populations has been reported for only few species (e.g. Tsuji et al. 2008). Daily travel distance does vary seasonally, but as costs of travel per day are only a minor portion of the daily energy expenditure in primates (Altmann 1998), we assume that we are allowed to ignore variation in energy expenditure for our purpose.

Ideally, we would use diet variability, brain size and body mass of the same population for each primate species. However, diet composition has generally been studied in different populations than the specimens available in museums from which brain sizes were measured. Therefore, we also compiled values of brain size and body mass sampled within a 100 km radius of the population in which diet composition was studied. Because the results from this reduced, conservative dataset (N=26 see Table A2) did not differ from those derived from a larger dataset containing the species averages of brain size and body mass (N=36), all of the results presented here are based on the larger dataset.

Cognitive Buffering (ENV-XPR) and environmental seasonality (ENV)

As a proxy for food availability we extracted several measures of environmental variables from remote sensing databases. Precipitation and temperature seasonality were extracted from the WorldClim data base (Hijmans et al. 2005) using ArcGIS 9.1 and a more direct measure of seasonality in plant productivity, the Normalized Difference Vegetation Index (NDVI, see Myneni et al. 2005), from the GIMMS database (Tucker et al. 2005). First, from monthly precipitation means we calculated the coefficient of variation (CV= SD/mean); the mean vector length (*r*), that estimates the concentration of precipitation over the year (Batschelet 1981); and P2T, a measure of the length of the dry season, where a dry month has a total precipitation (mm) that is less than two times the mean temperature (˚C) (Walter 1971). Second, we calculated SD among monthly mean temperatures. And finally we calculated the CV among months in the NDVI as a more direct measure of seasonality in plant productivity (Pettorelli et al. 2005) than the climatic variables.

To estimate the extent of cognitive buffering, we calculated the difference between the seasonality of the environment and the experienced seasonality (ENV-XPR). The measures of

environmental seasonality were extracted from the locations of the study populations for which dietary data were reported. Animals that buffer more will have a large difference (ENV-XPR), since they are able to keep their energy intake (XPR = experienced seasonality) more constant than expected on the basis of the seasonality in their habitat (ENV = environmental seasonality). To calculate this difference, we subtracted CV in diet (XPR) from either CV in plant productivity (NDVI; ENV1) or from CV in precipitation (ENV2).

Climatic data and plant productivity were additionally compiled (see above for details) for all the species for which we had a measure of female brain size and body mass (N=70 species, see Table A3.1). Locations from which these environmental data were taken from were matched to the locations where the specimens' endocranial volumes originated from.

Analyses

We controlled for phylogenetic relatedness using least-squared regressions (PGLS) analyses in R (R Development Core Team 2010) with the CAIC package (Orme et al. 2009). Phylogeny was based on version 2 of the consensus tree from the 10K Trees Project (Arnold et al. 2010) with *Colobus satanas, Procolobus verus, Piliocolobus kirkii, Cercopithecus stuhlmanni, C. pogonias and Semnopithecus priam* added according to Bininda-Emonds et al. (2007), *Presbytis spp.* according to Meijaard and Groves (2004), *Trachypithecus vetulus* according to Osterholz et al. (2008) and *Gorilla beringei* according to Jensen-Seaman et al. (2003) (Figure A3.1). All continuous variables were log-transformed before analysis, and statistical tests were parametric least-squares regressions, using R. In all multiple regressions, body mass was included as a covariate. Degree of folivory, group size, home range size, geographical range, gestation length and mating system have been shown to correlate with brain size in primates (e.g. reviewed in Healy and Rowe 2007). Hence we built models including these variables to eliminate their possible confounding effects. We estimated degree of folivory as yearly average percentage of leaves in the diet and group size as the average for the population concerned (values and sources are listed in the Appendix of this chapter). To choose the best fit from a set of models, we followed the standard approach (e.g. Richards 2005) of comparing the AIC (Information Theory Criterion, Akaike 1974) of different models. A lower AIC value indicates a better fit of the model to the data.

As the parameter lambda was close to 1 in most best-fit models, indicating a strong phylogenetic component in the data, usage of a phylogenetic method is required (Pagel 1999).

Bivariate plots of seasonality measures vs. residuals of brain size against body mass are shown for illustration, both using species means and independent contrasts.

Results

First, as predicted by the Expensive Brain hypothesis and controlling for the effect of body mass, brain size was negatively correlated with experienced seasonality, as measured by variation in dietary consumption (Figure 3.2a and b, Table 3.1a). Controlling for various covariates had little influence on the significance of the effect and did not improve the fit of the model (Table A3.3). This result indicates that species that experienced greater seasonality in their dietary energy intake had smaller brains relative to their body mass than species that experienced less seasonality in their diet.

Second, in concurrence with the Cognitive Buffer hypothesis, relative brain size was significantly positively correlated with the amount of cognitive buffering as measured by the difference between experienced seasonality and the seasonal variation in plant productivity (Figure 3.2c and d, Table 3.1b), and nearly so when precipitation is used instead. Again, including possible confounding variables did not affect these results (Table A3.3). Species that exhibited less variation in their energy intake than in their environment had larger brains relative to their body mass.

Furthermore, we looked at the relationship between environmental seasonality and brain size. None of the environmental variables were correlated with relative brain size (Figure 3.2 e and f, Table 3.1c). The enlarged sample of the 70 species yielded very similar results (Table A3.4).

Finally, there was no relationship between environmental seasonality and experienced seasonality (experienced seasonality vs. CV in precipitation N=36, r^2=0.01, p=0.5; experienced seasonality vs. CV in NDVI, r^2=0.04, p=0.3), showing that catarrhine primates do not follow the seasonality of their habitat in their energy intake.

Table 3.1. Phylogenetic least squared regressions (PGLS) testing for possible effects of seasonality on brain size. Each predictor variable was tested separately along with ln body mass (results not shown, $p<0.0001$ in all cases). Relationships are shown between relative brain size and (a) variation in diet, (b) environmental variation relative to diet variation, and (c) environmental seasonality for 36 nonhuman catarrhine primates.

	Phylogenetic signal (λ)	**t-value**	***P***	**AIC**
(a) Expensive Brain framework				
Experienced seasonality (XPR): CV in diet	0.99	-3.39	0.002	-60.9
(b) Cognitive Buffer hypothesis				
Buffer (ENV1-XPR): CV in plant productivity – CV in diet	0.99	3.28	0.002	-60.3
Buffer (ENV2-XPR): CV in precipitation – CV in diet	0.99	2.02	0.051	-54.4
(c) Environmental Seasonality				
CV in plant productivity (ENV1)	0.99	1.49	0.14	-60.2
CV in precipitation (ENV2)	0.99	0.63	0.53	-58.3
r in precipitation	0.99	0.45	0.66	-58.1
P2T	0.99	-0.55	0.59	-58.2
SD in temperature	0.99	0.24	0.81	-57.9

Note: Body mass was always included as a covariate. All lambdas are close to 1, which indicates that there was a strong phylogenetic component in the data and the necessity of applying a phylogenetic method (Pagel 1999).

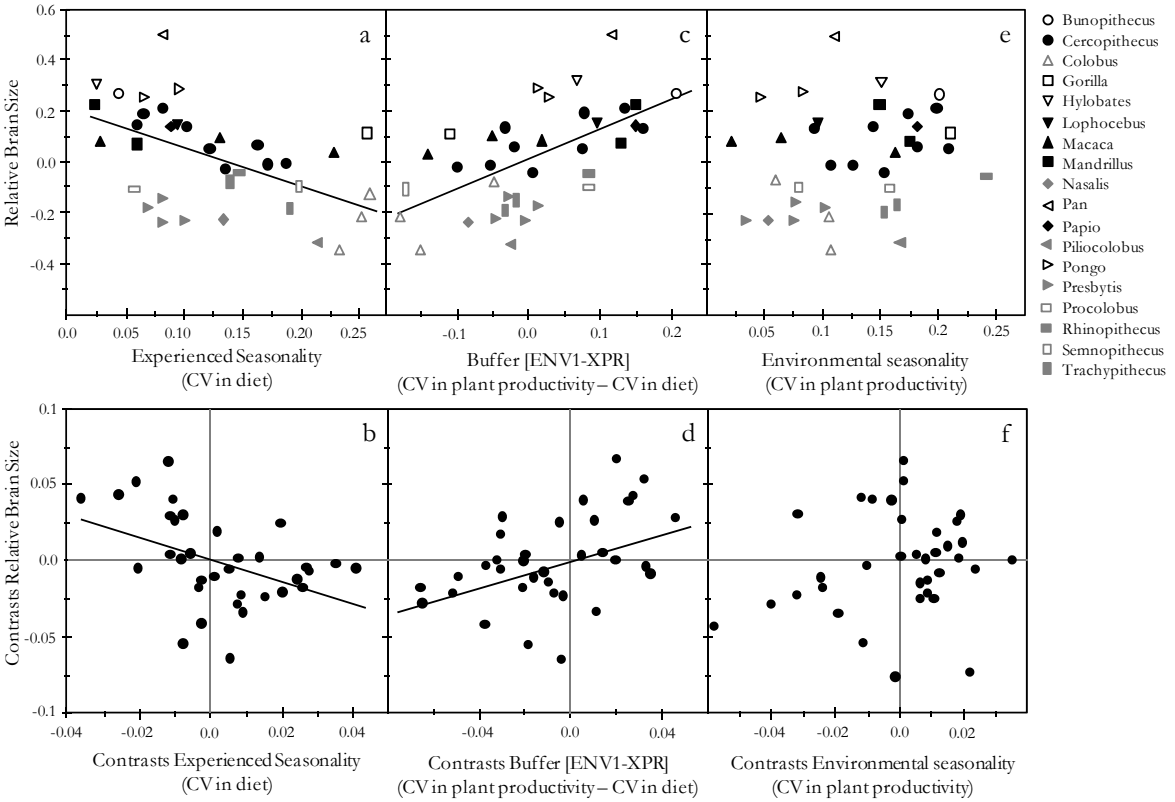

Figure 3.2. The influence of seasonality on relative brain size in nonhuman catarrhine primates. Species-level values are shown in the top panel, independent contrasts in the lower panel. As predicted by the Expensive Brain framework, experienced seasonality and brain size were negatively correlated (a and b). Additionally, there was a very strong cognitive buffering effect (c and d), as predicted by the Cognitive Buffer hypothesis. Consequently, no clear relationship was found between environmental seasonality and brain size (e and f), indicating that the effects tend to cancel each other. For statistical significance see Table 3.1.

Discussion

Species that experienced a higher degree of seasonality had a relatively smaller brain, suggesting that the energetic constraints due to seasonally induced food scarcity are an important factor in brain size evolution. This finding supports the Expensive Brain framework. However, relatively large-brained species exhibited more cognitive buffering, i.e. showed less seasonality in their diet consumption (experienced seasonality) than expected on the basis of environmental seasonality. This implies that cognitive buffering of environmental seasonality also operates, enabling larger-brained primates to live in these habitats despite the costs. This supports the Cognitive Buffer hypothesis, because exploiting varying food sources probably requires cognitive behavioral flexibility, such as switching to alternative food sources. Extractive foraging and tool use may be the most energetically rewarding behaviors used for cognitive buffering of environmental conditions, since they provide access to hidden and highly nutritional food items. Because what matters is the relative energetic costs of encephalization, it is irrelevant whether brains are larger relative to body mass or body mass is smaller relative to brain size. We did not test here whether seasonality in food intake is related to body mass alone, but of course this relationship is very likely also found in catarrhine primates (cf. Albrecht et al. 1990; Lehman et al. 2005). However, Isler and van Schaik (2009b) showed it is unlikely that the correlations between experienced seasonality and brain size, controlling for body mass, were in fact due to the "Economos-effect" (Economos 1980), i.e. because brain size is a better proxy of body size than body mass itself. Overall, our results indicate that energetic constraints and cognitive buffer effects tend to cancel each other in catarrhine primates, because we find no relationship between environmental seasonality and brain size.

Our results support the notion that larger-brained species may benefit from dealing with environmental change through behavioral flexibility. Thus, relatively large brains may have evolved to deal with novel ecological challenges, as is suggested in birds (Sol and Lefebvre 2000; Shultz et al. 2005; Sol et al. 2005a) and a broad range of mammals (Sol et al. 2008). However, here we show that to be able to benefit from these advantages, energetic costs need to be overcome to actually grow and maintain a larger brain.

In African strepsirrhine primates (lemurs and lorises), the energetic effect of seasonality on their relative brain size is very pronounced (van Woerden et al. 2010), whereas cognitive buffer effects are much weaker (PGLS: $p=0.14$, $\lambda=1.00$, Figure A3.2) than within catarrhine

primates. Energetic constraints prevail over cognitive buffering in the lemurs, as shown by consistent negative correlation between relative brain size and environmental seasonality (both climatic seasonality and plant productivity, see van Woerden et al. 2010). In other words, experienced seasonality more closely reflects habitat seasonality in strepsirrhines compared to the catarrhine primates. The different pattern of results for the two lineages might be due to differences in the distribution of energetic costs between small and large primates. Extant strepsirrhines devote a relatively larger percentage of basal metabolism to brain maintenance (11-12%) compared to larger primates (8-9% in cercopithecoid primates, calculated from Mink et al. 1981; Isler et al. 2008, see Figure 3.3). Therefore, the threshold for the effectiveness of cognitive buffers to overcome the energetic constraints of increasing brain size may be higher in strepsirrhines (and other small primates such as callitrichines) compared to the larger monkeys or apes. However, a difference in body mass is unlikely to be the only factor, because this does not explain why most of the much larger-bodied extinct lemur species also had relatively small brains compared to catarrhines (Schwartz et al. 2005). An alternative explanation is that perhaps lemurs show more limited cognitive buffering because they more often face periods of unavoidable starvation, an idea supported by the many adaptations to cope with long periods of food scarcity. Thus, the only hibernating primates are found among lemurs (Schülke and Ostner 2007), and all lemurs are seasonal breeders, except the large-brained aye-aye (Sterling 1994), which is an extractive forager.

The two hypotheses presented in this paper, the Expensive Brain framework, and the Cognitive Buffer hypothesis, are nonexclusive and both turn out to be crucial to disentangle the relationship between seasonality and brain size. They both affect how relative brain size responds to environmental seasonality, and can therefore be integrated as follows (Figure 3.4): If the energetic constraints predominate, a negative correlation is found (dashed line, dark grey area, Figure 3.4). If the cognitive buffer effect predominates, a positive correlation is found (dotted line, light grey area, Figure 3.4). If both effects tend to cancel each other, there is no clear correlation between environmental seasonality and brain size (black area, figure 3.4).

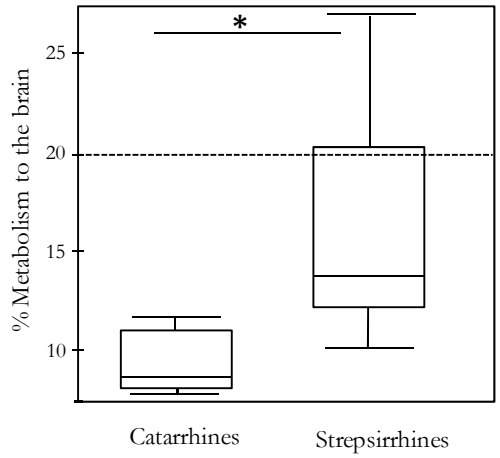

Figure 3.3. The relative energetic cost of strepshirrhine brains exceeds that of catarrhines (ANOVA: $F(1,13) = 5.23$, $p=0.038$), some Strepsirrhines allocate a similar proportion of their metabolism to their brain as humans do (dashed line, Holliday 1971). The percentage of basal metabolic rate (BMR) used for the brain was estimated from calculating brain metabolic rates per gram of brain tissue (Mink et al. 1981). BMR values of primate species were taken from McNab (2008). Metabolic consumption of the brain mass was then divided by basal metabolic consumption of the body.

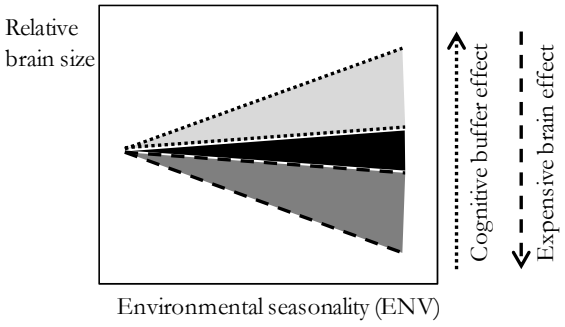

Figure 3.4. The predictions of the two hypotheses, the Expensive Brain framework and the Cognitive Buffer hypothesis, presented in this article can be integrated into one graphical representation between environmental seasonality and brain size. A negative correlation will be found if energetic constraints prevail (dark grey area), whereas if cognitive buffer effects are most important a positive correlation will be found (light grey area). If these effects are equally strong, there will be no correlation between environmental seasonality and brain size (black area).

We expect the effects of energetic constraints to prevail if animals cannot move into other habitats, or if a dietary switch to explore hidden high-quality food sources is somehow prevented (e.g. extractive foraging). A high energy consumption of the brain relative to total metabolism and a high extrinsic (unavoidable) mortality further reduce the possible benefits of a cognitive buffer. Thus, we expect cognitive buffer effects to be most apparent in the following categories of animals: (i) animals that can fly or swim and thus easily sample other habitats or move into other regions, such as birds, bats and some classes of marine mammals, (ii) animals that can more easily cope with minor reductions in food availability because their brains usurp only a relatively modest portion of the energy budget, in particular due to large body size, such as large carnivores; and (iii) animals that rely on extractive foraging, food caching, or that exploit dispersed food patches. These predictions are in accordance with previous findings on birds. In temperate Palearctic temperate birds, cognitive buffer effects prevail over energetic constraints (Sol et al. 2005b; Sol et al. 2007). Furthermore, in South-American parrots there is a direct positive relationship between environmental seasonality and relative brain size (Schuck-Paim et al. 2008), also hinting at a prevalence of cognitive buffer effects over energetic constraints. In lineages lacking these features, especially smaller non-volant mammals, the expensive brain effects should predominate, leading to a negative correlation between both environmental and experienced seasonality and brain size.

Both the cost and the benefits perspectives concern energy acquisition i.e. are explicitly ecological. They explain a reasonable amount of variation in brain size and thus support ecological approaches to brain size evolution (Byrne 1997), although they must be tested in more detail using direct measures of food availability instead of using environmental seasonality as a proxy. It is not clear whether the social benefits of brain size increases (Dunbar 1998) will account for additional variation in brain size once these ecological effects are factored in. Future studies should try to integrate all perspectives to assess their relative importance.

Overall, this study shows the importance of incorporating both costs and benefit perspectives in models on brain size evolution. In catarrhine primates, cognitive buffers just manage to level out the energetic constraints of the environmental seasonality. For any species, we must carefully consider the magnitude of these effects separately. The evolution of early hominins may be an example of how cognitive buffering can surmount energetic constraints. On the other hand, cognitive buffering may not be an option in a restricted island habitat like the one

of *Homo floresiensis* or if severe nonperiodic droughts, like El-Niño effect in the East Borneo for *Pongo pygmaeus morio,* lead to unavoidable periods of starvation.

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Appendix Chapter 3

Table A3.1. List of species and their specific data used in this study.

Species	BoM (g)	ECV (ml)	N ECV	CV in diet	Diet Study Location	% LV in diet	CV in Prec†	CV in NDVI†	Diff (CV in NDVI†)	Diff (CV in Prec†)	Group size†	HR (ha)§	Mating system§	Gest. (d)	GeoR (deg. Lat)€	P2T	CV in Prec‡	r in Prec‡	SD in Temp‡	CV in NDVI‡
Bunopithecus hoolock	6350*	106.6 ±9.2	11	0.045	Lawachara, Bangladesh[1]	6.3	0.830	0.25	0.206	0.785	3.5		0		10.15	8.8	0.907	0.608	40.4	0.201
Cercocebus atys	6200[52]	85.9 ±7.8	10													12.0	0.560	0.315	6.3	0.156
Cercopithecus albogularis	4262*	66.2 ±8.1	20													9.5	0.736	0.333	16.0	0.138
Cercopithecus ascanius	2902*	56.7 ±5.6	25	0.102 ±0.06	Budongo Forest, Uganda[2]; Kakamega, Kenya[3]	27.5	0.380	0.070	-0.04	0.278	22	3.2	1	172[55]	22.19	11.2	0.386	0.176	4.8	0.095
Cercopithecus campbelli	2545*	54.9 ±5.7	21	0.064	Tai Forest, Cote d'Ivoire[4]	12.3	0.490	0.142	0.078	0.426	9	21.5	1	180[56]	10.87	11.1	0.580	0.324	7.6	0.175
Cercopithecus cephus	2880[52]	60.7 ±8.4	17	0.083 ±0.002	Makokou[5]; Lope Reserve[6], Gabon	7.9	0.650	0.216	0.133	0.567	6	34	1	170[55]	12.64	9.2	0.625	0.256	10.0	0.198
Cercopithecus diana	3900[52]	57.3 ±4.8	14	0.136	Tai Forest, Cote d'Ivoire[4]	18.5	0.490	0.142	0.006	0.354	24	105.5	1		5.82	11.1	0.584	0.308	7.6	0.154
Cercopithecus lhoesti	3450[52]	66.5 ±4.8	12													11.7	0.347	0.157	4.7	0.081
Cercopithecus lowei	2097*	51.2 ±6.1	6													9.3	0.648	0.323	10.1	0.378
Cercopithecus mitis	4629*	65.8 ±6.5	34	0.188 ±0.08	Zomba plateau, Malawi[7]; Budongo Forest, Uganda[2]; Kakamega, Kenya[3]	35.9	0.580	0.089	-0.1	0.388	27	83.8	1	176[57]	25.42	9.9	0.504	0.287	7.2	0.127
Cercopithecus mona	1920*	55.9 ±2.8														10.7	0.663	0.404	8.7	0.166
Cercopithecus nictitans	4260[52]	66.8 ±7.9	21	0.122 ±0.05	Makokou[5]; Makande[8]; Lope Reserve[6], Gabon	13.6	0.660	0.195	0.073	0.538	13.5	120.5	1	170	15.43	9.9	0.556	0.216	8.4	0.209
Cercopithecus petaurista	2919*	52.7 ±7.3	27	0.163	Tai Forest, Cote d'Ivoire[4]	43.6	0.490	0.142	-0.02	0.327	10		1		7.63	11.0	0.567	0.314	8.1	0.180
Cercopithecus pogonias	2900[52]	56.5 ±5.0	12	0.06 ±0.01	Makokou[5]; Makande[8], Gabon	8.0	0.650	0.221	0.160	0.585	14	103	1	170	11.88	9.7	0.573	0.313	8.5	0.144

Cercopithecus stuhlmanni	4629*	65.8 ±6.4	19	0.172	Budongo, Uganda[9]	34.9	0.400	0.116	-0.06	0.228	~27		1		21.06	10.5	0.451	0.238	6.4	0.108
Cercopithecus wolfi	2870[52]	58.3 ±4.4	9													11.4	0.328	0.128	4.6	0.085
Chlorocebus aethiops	3039*	57.0 ±6.6	27													7.9	0.783	0.440	12.5	0.260
Chlorocebus pygerythrus	3576*	59.9 ±5.6	34													7.3	0.819	0.484	22.6	0.185
Colobus angolensis	7849[52]	65.8 ±5.6	5	0.233	Nyungwe forest, Rwanda[10]	81.0	0.500	0.079	-0.15	0.267	>300		2		15.55	10.5	0.508	0.166	9.0	0.107
Colobus guereza	7503*	72.6 ±6.1	30	0.25 ±0.08	Kakamega, Kenya[11]; Budongo Forest, Uganda[2]	61.4	0.385	0.066	-0.19	0.135	8	12.6	2	158[58]	15.39	10.8	0.496	0.211	6.0	0.106
Colobus polykomos	6708*	71.0 ±4.7	28	0.259 ±0.002	Tai Forest, Cote d'Ivoire[12] ; Tiwai Island, Sierra Leone[13 ; 14]	56.9	0.643	0.149	-0.02	0.471	13.6	36	2	170[59]	8.65	11.0	0.572	0.318	8.0	0.165
Colobus vellerosus	7220*	69.0 ±4.0	6													9.2	0.580	0.313	10.8	0.247
Gorilla beringei	97500[52]	469.7 ±22.5	8													11.3	0.420	0.170	2.4	0.120
Gorilla gorilla	71500[52]	434.4 ±45.6	33	0.257 ±0.06	Bai Hokou[15]; Mondika, CAR[16]; Nouabale-Ndoke reserve, Congo[17]	61.0	0.406	0.147	-0.11	0.149	9	2544	1	257[55]	12.83	10.1	0.578	0.202	8.0	0.211
Hylobates agilis	5820[52]	87.9 ±10.8	15													12.0	0.280	0.141	3.4	0.054
Hylobates klossii	5920[52]	88.5 ±6.5	10													12.0	0.269	0.164	2.8	0.100
Hylobates lar	5383*	100.1 ±8.6	108	0.025	Ketambe, Indonesia[18]	3.2	0.330	0.093	0.068	0.305	5	34.2	0	213[55]	23.08	7.7	0.765	0.483	22.3	0.152
Hylobates muelleri	5670*	92.8 ±8.9	37													12.0	0.238	0.142	3.5	0.066
Hylobates pileatus	5440[52]	90.5 ±6.2	9													7.8	0.784	0.442	13.0	0.091
Lophocebus albigena	5976[53]	90.7 ±7.5	33	0.095 ±0.07	Dja Reserve, Cameroon[19]; Makande, Gabon[8]	9.1	0.615	0.191	0.096	0.520	15	250	2	175[55]	13.47	10.9	0.410	0.188	6.2	0.096
Macaca assamensis	7031[52]	89.6 ±12.7	10													7.1	0.895	0.592	28.0	0.142
Macaca fascicularis	3516*	61.0 ±6.0	99	0.130 ±0.06	Kutai National Reserve[20]; Ketambe[2]; Tanjung Puting[21], Indonesia	16.7	0.290	0.079	-0.05	0.160	27	69.3	2	163[60]	31.47	11.4	0.415	0.263	5.8	0.064

Macaca fuscata	8030[52]	97.9 ±13.8	6	0.227	Yakushima, Japan[22-25]	31.8	0.450	0.085	-0.14	0.223	12	177.1	2	173[55]	14.01	12.0	0.450	0.292	76.5	0.164
Macaca hecki	6800[52]	94.6 ±8.4	5													12.0	0.190	0.069	3.2	0.029
Macaca mulatta	5670*	82.2 ±13.2	37													8.7	0.870	0.564	40.1	0.186
Macaca nemestrina	6539*	98.6 ±8.8	20													11.8	0.301	0.175	6.1	0.066
Macaca nigra	5470[52]	80.2 ±7.4	10	0.028	Tangkoko-Dua Sudara Nature Reserve[3]	2.1	0.310	0.045	0.017	0.282	67	260	2	176[60]	0.38	12.0	0.338	0.221	3.6	0.026
Macaca sylvanus	9625[1]	94.8 ±7.1	10													8.0	0.644	0.429	51.9	0.183
Macaca tonkeana	9000[52]	93.7 ±6.3	11													12.0	0.304	0.191	3.6	0.041
Mandrillus leucophaeus	8840*	126.3 ±15.2	7	0.025	Korup Nat Park, Cameroon[26]	27.7	0.580	0.174	0.149	0.555	77	500	1	173[55]	3.69	9.2	0.662	0.387	9.6	0.149
Mandrillus sphinx	12800[54]	137.3 ±20.2	6	0.060	Mvini village, Cameroon[27]	8.2	0.580	0.190	0.130	0.520	95	500	1	175[55]	7.98	9.8	0.595	0.300	8.8	0.178
Nasalis larvatus	9730*	84.9 ±6.8	28	0.134 ±0.01	Menanggul River[28]; Tanjung Puting[29], Indonesia	46.0	0.250	0.049	-0.09	0.116	12.7	261	1	166[55]	10.0	12.0	0.267	0.161	3.9	0.052
Nomascus gabriellae	7320[52]	115.8 ±5.8	7													8.7	0.900	0.603	15.9	0.101
Pan t. schweinfurthii	33700[52]	391.6 ±37.1	11	0.083	Gombe, Uganda[30]	25.4	0.740	0.202	0.119	0.657	44	1787	2	235[55]	13.64	10.9	0.388	0.179	5.8	0.113
Papio anubis	14969*	153.5 ±14.4	23													9.6	0.495	0.236	7.8	0.164
Papio cynocephalus	13121*	149.6 ±14.0	13	0.091 ±0.06	Amboseli National Park, Kenya[31]; Mikumi National Park, Tanzania[32; 33]	45.7	0.810	0.246	0.156	0.719	56	4564	2	175[55]	24.25	8.0	0.724	0.396	11.1	0.185
Piliocolobus badius	7130*	63.7 ±7.8	38	0.214 ±0.07	Tai Forest, Cote d'Ivoire[12]; Botsima[34]; Mchelelo[35], Kenya; Gombe, Tanzania[36]; Tiwai Island, Sierra Leone[14]	51.6	0.528	0.149	-0.02	0.357	34.3	57.5	2	174[61]	10.86	10.5	0.646	0.351	8.3	0.170
Pongo abelii	41151*	349.7 ±25.9	19	0.065	Ketambe, Indonesia[37]	21.8	0.330	0.093	0.028	0.265	1.5	600	2	243[62]	5.35	12.0	0.272	0.154	3.9	0.046
Pongo p. wurmbii	36754*	334.6 ±30.4	31	0.095 ±0.01	Gunung Palung[38]; Tanjung Putting[39]; Tuanan[2], Indonesia	48.0	0.330	0.107	0.012	0.235	1	300	2	250[55]	9.87	12.0	0.247	0.147	3.0	0.083

Presbytis comata	6710[52]	67.7 ±4.5	9													12.0	0.520	0.359	3.4	0.153
Presbytis frontata	6889*	73.1 ±5.6	7													12.0	0.203	0.117	2.4	0.063
Presbytis hosei	5630[52]	60.0 ±3.8	9	0.082	Off the Semaga river, Indonesia[40]	62.0	0.240	0.036	-0.05	0.158	5.5		1		8.38	12.0	0.204	0.107	3.3	0.074
Presbytis melalophos	6567*	61.3 ±5.2	22													12.0	0.263	0.152	3.1	0.070
Presbytis potenziani	4817[52]	57.0 ±4.6	8	0.068	Muntei, N Pagi Isl, Indonesia[41]	23.4	0.280	0.081	0.013	0.212	6		1		3.39	12.0	0.268	0.162	2.8	0.102
Presbytis rubicunda	6223*	68.8 ±4.5	31	0.081 ±0.09	Sepilok Virgin Jungle Reserve, Malaysia[42; 43]	39.0	0.170	0.051	-0.03	0.089	6		1		10.22	12.0	0.259	0.146	3.7	0.075
Presbytis siamensis	6366*	57.2 ±8.7	7													12.0	0.193	0.082	3.3	0.078
Presbytis thomasi	6350*	64.7 ±6.1	5	0.100	Ketambe, Indonesia[18]	52.6	0.330	0.093	-0.01	0.230	8	37.7	1	167.7	3.12	12.0	0.280	0.153	4.4	0.035
Procolobus verus	3707*	51.6 ±3.8	14	0.058	Tai Forest, Cote d'Ivoire[12]	82.3	0.490	0.142	0.084	0.432	7.8	26.5	2	180[61]	5.38	11.6	0.549	0.296	7.2	0.160
Rhinopithecus roxellana	11600[52]	114.3 ±3.9	9	0.146	Qianjiaping, Hubei prov, China[44]	73.0	0.60	0.231	0.085	0.455	120		2		3.4	11.0	0.834	0.567	64.2	0.315
Semnopithecus dussumieri	10130*	88.3 ±3.6	6													6.2	1.008	0.630	21.3	0.233
Semnopithecus priam	6575*	75.3 ±5.6	7	0.199	Polonnaruwa, Sri Lanka[45]	54.7	0.730	0.026	-0.17	0.531	~9		1		9.48	9.3	0.837	0.437	13.5	0.080
Simias concolor	7031*	52.5 ±5.1	6													12.0	0.265	0.161	2.8	0.098
Symphalangus syndactilus	10745*	122.4± 11.2	34													12.0	0.312	0.189	3.5	0.065
Trachypithecus auratus	9525*	63.6 ±3.7	17													12.0	0.529	0.361	5.1	0.124
Trachypithecus cristatus	6060*	57.4 ±6.2	50													11.6	0.312	0.182	4.8	0.064
Trachypithecus obscurus	6765*	59.8 ±4.3	31													11.7	0.359	0.182	4.3	0.028
Trachypithecus phayrei	7182*	70.1 ±7.6	26													7.2	0.823	0.547	26.7	0.180
Trachypithecus pileatus	11340*	97.3 ±9.8	11	0.189 ±0.02	Madhupur Nat Park, Bangladesh[46]; Pakhui Wildlife Sanctuary, India[47]	55.0	0.877	0.157	-0.03	0.687	9	42.5	1		7.17	8.4	0.958	0.639	38.2	0.154
Trachypithecus vetulus	7459*	83.7 ±5.9	7	0.138 ±0.1	Polonnaruwa[45]; Panadura[48], Sri Lanka	44.6	0.500	0.090	-0.05	0.362	13	4.4	1	200[55]	7.26	12.0	0.430	0.130	5.8	0.059

Note: BoM = female body mass, ECV = female endocranial volume (for more details on the dataset, see [49]), N ECV = number of female endocranial volumes averaged, CV = coefficient of variation, LV = leaves, Prec = precipitation, NDVI = Normalized Difference Vegetation Index, P2T = number of dry months, *r* = the mean vector length, an estimate of the concentration of precipitation over the year, SD = standard deviation, Temp = temperature, HR = home range, Gest = gestation lenght, GeoR = geographical range. Diff (CV in NDVI) = the difference between CV in diet and CV in NDVI[†], a measure of the amount of buffering taking place, see main text. Diff (CV in Prec) = the difference between CV in diet and CV in Prec[†], a measure of the amount of buffering taking place, see main text.

[†] Environmental data and group size data were taken from same study location as dietary data. [‡]Environmental data taken from same locations as endocranial volumes were originally from.

[$] Home range data are from Wich and Nunn [50].

[§] Mating systems: 0 =Monogamous, 1=Unimale, 2=Multimale. Data from Lindenfors and Tullberg [51]

[€] Geographical range: maximal distance in latitudinal degrees of the distribution range of the species was taken (source distribution: IUCN redlist)

[*]Body mass taken from same specimens as ECV measurements,

[1]Pastorini personal communication

[2]Carel van Schaik & Maria van Noordwijk, unpubl.

[3]O'Brien and Kinnaird personal communication.

Table A3.2. Multivariate phylogenetic least square regressions (PGLS) between seasonality and brain size, controlling for body mass using a reduced data set of average brain sizes from individual specimens collected within a 100 km radius of the study location from which dietary data was taken for that species (N=26).

	Phylogenetic signal (λ)	**t-value**	***P***	**AICl**
(a) Expensive Brain framework				
Experienced seasonality: CV in diet	0.63	-2.91	0.007	-21.3
(b) Cognitive Buffer hypothesis				
Buffer [ENV1-XPR]: CV in plant productivity – CV in diet	0.64	3.09	0.005	-22.2
Buffer [ENV2-XPR]: CV in precipitation – CV in diet	0.89	3.12	0.005	-23.0

Note: All lambda (λ) values were significantly different from 0, indicating a strong phylogenetic effect.

Supplementary Text A3.1: Confounding variables

We tested for a number of possible correlates of brain size [cf. 63] whether their inclusion as a covariate affected the correlations between brain size and experienced seasonality (CV in diet), or the two measures of cognitive buffering (CV in plant productivity [ENV1]- CV in diet; CV in precipitation [ENV2] – CV in diet). For each covariate, we briefly discuss whether and in which direction a confounding effect would be expected. Overall, the model with the lowest AIC, and thus the best fit model, is always the one without any covariates, except in the case of gestation length which is also the only variable that correlates significantly with brain size when controlling for body mass in our dataset.

1) Degree of folivory: More folivorous primate species have relatively small brains for their body mass compared to more frugivorous species [64, 65]. In seasonal habitats, fruit availability fluctuates more than leaf availability, and species tend to be more folivorous overall. Therefore we would expect frugivores to exhibit lower experienced seasonality and a larger amount of cognitive buffering (and thus a negative correlation of the degree of folivory with ENV-XPR, but a positive correlation with XPR). We find support for both these predictions; degree of folivory is strongly positively correlated with experienced seasonality and negatively correlated with the amount of cognitive buffering (Table A3.3).

As a consequence, the degree of folivory might be the underlying factor leading to a spurious positive correlation between brain size and the amount of cognitive buffering and a spurious negative correlation between experienced seasonality and brain size. Indeed, the results of the combined model including the degree of folivory as a covariate show a slightly decreased effect of the amount of cognitive buffering on brain size (but not changing its level of significance), but not on the effect of experienced seasonality (Table A3.3).

2) Group size: In primates, group size has been shown to positively correlate with neocortex ratio, which correlates tightly with overall brain size [66]. On the other hand, habitat seasonality may affect group size in both directions, depending on the species and the situation [67].

In our sample, group size is not correlated with brain size (controlling for body mass) or with our seasonality measures, and is therefore not affecting the effects of experienced seasonality or cognitive buffering on brain size. Incidentally, the absence of a positive correlation

between group size and brain size (controlling for body mass) in our sample should not be interpreted as evidence against the social brain hypothesis, as data on both group size and brain size are available for many more species.

3) Home range size and geographic range: It has been proposed that species with relatively large brains and thus higher cognitive abilities can remember more resource locations and thus are able to exploit larger home ranges [68] or, as a species, inhabit a broader geographic range. On the other hand, species living in more seasonal habitats are forced to range further in lean periods to find sufficient food [69], and a geographic range spanning more degrees of latitude is likely to include more seasonal habitats. Thus, home range size or geographical range may be the underlying factor responsible for a positive correlation between brain size and habitat seasonality. However, in our sample of species, we did not find an effect of home range size or geographic range on brain size or on any of our measures of seasonality; and thus there was no confounding effect of these covariates on our results.

4) Mating system: In other mammalian orders, species that exhibit monogamous pair bonds have larger brains than non-monogamous species [70]. However, in primates, the largest relative brain sizes are found in species with a multi-male mating system [70]. In our sample we find no relationship of mating system with brain size, but a trend of increased experienced seasonality from monogamous to one-male to multi-male mating systems. However, when we included mating system as a covariate, this did not affect our results.

5) Gestation length: Gestation length has been shown to positively correlate with brain size [71], and this is confirmed in our sample (Table A3.3). Rather than on gestation, constraints of environmental seasonality on development periods are most pronounced for the timing and length of lactation, as this period is most costly for the mother, and the timing of weaning, as the juvenile period is most costly for the offspring. Gestation on the other hand is often timed to take place during relatively lean periods. However, gestation may be prolonged in adverse conditions [72]. Thus, we would expect species in highly seasonal environments to exhibit longer gestation lengths. But if the correlation between gestation length and brain size is indeed an energetic issue, we would not expect larger brains if the gestation period is prolonged due to poor nutritional state

of the mother. Nevertheless, we included gestation length as a covariate in our models, as it is significantly correlated to brain size in our sample. This covariate did not affect our results either.

Overall we can conclude that none of the covariates interfere with our results, indicating a robust energetic constraint and cognitive buffer effect of seasonality on brain size evolution in catarrhine nonhuman primates.

Table A3.3. Phylogenetic least squared regressions (PGLS) with brain size as the response variable, one of the three seasonality variables (experienced seasonality, buffer 1 and buffer 2) as effect variable, and including each possibly confounding covariate separately.

A) **Expensive Brain**		**Combined model**					**Covariate alone**			
		CV in diet (XPR)		**Covariate**			**with XPR**		**with relative brain**	
Covariate	**N**	**t-value**	***P***	**t-value**	***P***	**AIC of total model**	**t-value**	***P***	**t-value**	***P***
none (no covariate)	36	-3.39	0.002			-60.9				
degree of folivory	36	-2.76	0.009	-0.93	0.36	-58.8	4.15	<0.0002	-1.98	0.06
ln group size	36	-3.35	0.002	-1.48	0.15	-60.2	0.10	0.92	-0.95	0.35
geographical range	36	-3.42	0.002	0.67	0.51	-58.3	1.15	0.26	0.14	0.89
mating system	36	-3.37	0.002	1.13	0.27	-59.2	1.77	0.09	1.09	0.29
none (reduced N)	29	-3.46	0.002			-46.3				
ln home range size	29	-3.23	0.003	0.45	0.65	-43.4	0.20	0.84	0.99	0.33
none (reduced N)	24	-2.95	0.008			-32.5				
ln gestation length	24	-2.79	0.009	2.19	0.04	-34.5	1.20	0.22	2.22	0.04

B) **Cognitive Buffer ENV1**		**Combined model**					**Covariate alone**	
		CV in **plant productivity (ENV1)** – XPR		**Covariate**			**with ENV1-XPR**	
Covariate	**N**	**t-value**	***P***	**t-value**	***P***	**AIC of total model**	**t-value**	***P***
none	36	3.28	0.002			-60.3		
degree of folivory	36	2.67	0.012	-1.02	0.32	-58.4	-3.49	0.001
ln group size	36	3.22	0.003	0.14	0.89	-57.2	0.95	0.35
geographical range	36	3.58	0.001	1.34	0.19	-59.2	-0.93	0.36
mating system	36	3.17	0.003	0.92	0.36	-58.2	-1.02	0.32
none (reduced N)	29	2.90	0.007			-43.4		
ln home range size	29	2.76	0.01	0.03	0.98	-29.5	0.12	0.90
none (reduced N)	24	2.99	0.007			-32.7		
ln gestation length	24	2.86	0.01	2.10	0.05	-34.3	-1.82	0.08

Table A3.3. Cont.

C) **Cognitive Buffer ENV2**		**Combined model**					**Covariate alone**	
		CV in **precipitation (ENV2)** – XPR		**Covariate**			**with ENV2-XPR**	
Covariate	**N**	**t-value**	***P***	**t-value**	***P***	**AIC of total model**	**t-value**	***P***
none	36	2.02	0.05			-54.4		
degree of folivory	36	1.84	0.08	-1.76	0.09	-54.6	-1.48	0.15
ln group size	36	1.98	0.06	-0.02	0.98	-51.2	1.66	0.11
geographical range	36	2.10	0.04	0.66	0.51	-51.8	-0.30	0.77
mating system	36	1.94	0.06	0.97	0.34	-52.3	-0.67	0.77
none (reduced N)	29	1.79	0.09			-38.7		
ln home range size	29	2.46	0.02	0.02	0.98	-28.1	-0.19	0.51
none (reduced N)	24	2.68	0.01			-31.3		
ln gestation length	24	2.53	0.02	2.07	0.05	-32.8	-1.72	0.10

Note: In all cases body mass was included in the model (significance $p<0.0001$) and there was a strong phylogenetic effect (lambda was not significantly different from 1). The models do not differ greatly in their AIC values, and in all cases the significant relationships between relative brain size and our seasonality measures remain.

Table A3.4. Relationship between environmental seasonality and brain size, using all the species for which brain sizes and environmental data were available (N=70). Environmental data were extracted from locations which were matched to where the specimen's endocranial volumes originated from.

	Phylogenetic signal (λ)	**t-value**	***P***	**AIC Model**
Environmental Seasonality (N=70)				
CV in plant productivity (ENV1)	0.88	0.43	0.67	-92.4
CV in precipitation (ENV2)	0.88	1.03	0.30	-93.3
r in precipitation	0.89	1.10	0.28	-93.5
p2t	0.88	-0.75	0.46	-92.8
SD in temperature	0.89	1.17	0.24	-93.6

Note: All lambda values did not differ significantly from 1.

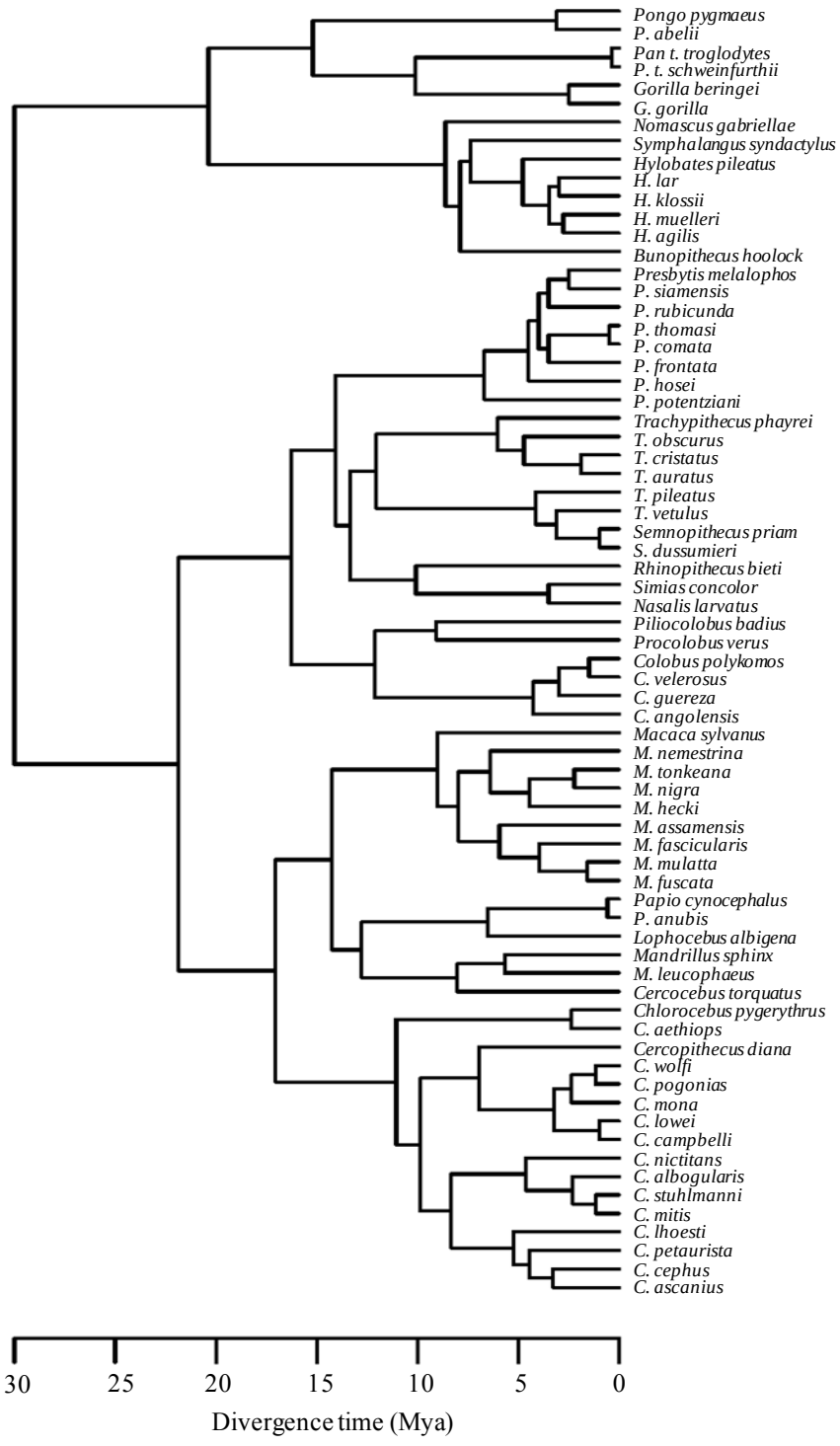

Figure A3.1. Phylogeny used to perform the phylogenetic least squared regressions (PGLS). For details see the methods section of the original paper.

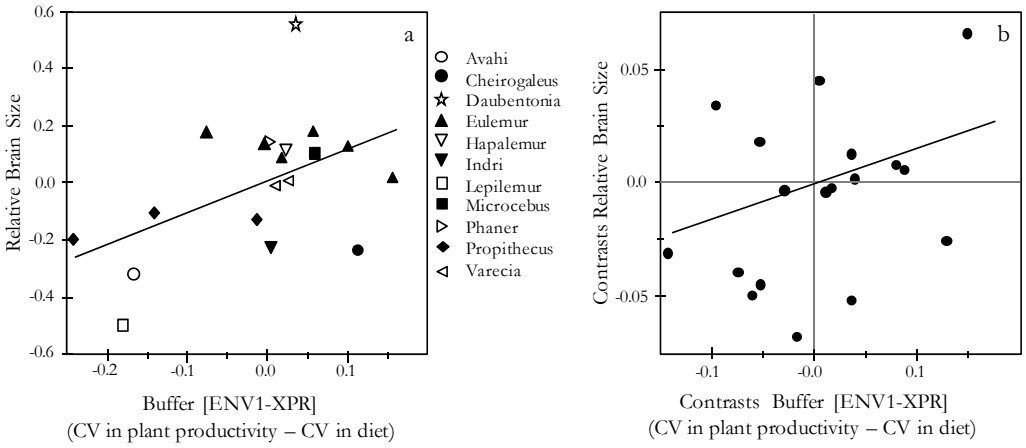

Figure A3.2. Buffering (difference between environmental seasonality and experienced seasonality) is only weakly positively correlated to relative brain size in Malagasy lemurs (PGLS: p=0.14, λ=1.00). Therefore there is only weak evidence for the Cognitive Buffer Hypothesis in this group [63].

References appendix Chapter 3

1. Islam, M. A. & Feeroz, M. M. 1992. Ecology of hoolock gibbon of Bangladesh. Primates 33, 451-464.
2. Plumptre, A. J. 2006. The diets, preferences, and overlap of the primate community in the Budongo Forest Reserve, Uganda. In Primates of Western Uganda (ed. N. E. Newton-Fisher, H. Notman, J. D. Paterson & V. Reynolds). New York: Springer.
3. Cords, M. 1986. Interspecific and intraspecific variation in diet of 2 forest guenons, *Cercopithecus. ascanius* and *C. mitis*. Journal of Animal Ecology 55, 811-827.
4. Buzzard, P. J. 2006. Ecological partitioning of *Cercopithecus campbelli, Cercopithecus petaurista,* and *Cercopithecus diana* in the Tai Forest. International Journal of Primatology 27, 529-558.
5. Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. Journal of Animal Ecology 49, 237-269.
6. Tutin, C. E. G. 1999. Fragmented living: Behavioural ecology of primates in a forest fragment in the Lope Reserve, Gabon. Primates 40, 249-265.
7. Beeson, M. 1989 Seasonal dietary stress in a forest monkey (*Cercopithecus mitis*). Oecologia 78, 565-570.
8. Brugiere, D., Gautier, J. P., Moungazi, A. & Gautier-Hion, A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. International Journal of Primatology 23, 999-1024.
9. Fairgrieve, C. & Muhumuza, G. 2003. Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni Matschie*) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. African Journal of Ecology 41, 141-149.
10. Fimbel, C., Vedder, A., Dierenfeld, E. & Mulindahabi, F. 2001. An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. African Journal of Ecology 39, 83-92.
11. Fashing, P. J. 2001. Feeding ecology of guerezas in the Kakamega Forest, Kenya: The importance of *Moraceae* fruit in their diet. International Journal of Primatology 22, 579-609.
12. Korstjens, A. H., Bergmann, K., Deffernez, C., Krebs, M., Nijssen, E. C., van Oirschot, B. A. M., Paukert, C. & Schippers, E. P. 2007. How small-scale differences in food competition lead to different social systems in three closely related sympatric colobines. In Monkeys of the Tai Forest (ed. W. S. McGraw, K. Zuberbühler & R. Noe). Cambridge: Cambidge University Press.

13. Dasilva, G. L. 1994. Diet of *Colobus polykomos* on Tiwai Island - Selection of Food in Relation to Its Seasonal Abundance and Nutritional Quality. International Journal of Primatology 15, 655-680.
14. Davies, A. G., Oates, J. F. & Dasilva, G. L. 1999. Patterns of frugivory in three West African colobine monkeys. International Journal of Primatology 20, 327-357.
15. Remis, M. J. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. American Journal of Primatology 43, 87-109.
16. Doran, D. & Greer, D. 2002. The influence of swamp use and fruit consumption on western gorilla (*Gorilla gorilla gorilla*) ranging behavior at Mondika Research Center. American Journal of Physical Anthropology, 64-65.
17. Nishihara, T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National-Park, Congo. Primates 36, 151-168.
18. Ungar, P. S. 1992. Incisor microwear and feeding behavior of four sumatran anthropoids, vol. PhD Thesis: State University of New York, Stony Brook.
19. Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. American Journal of Primatology 54, 91-105.
20. Wheatley, B. P. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In The Macaques: Studies in Ecology, Behavior and Evolution. (ed. D. G. Lindburg), pp. 215–246. New York: Van Nostrand Reinhold.
21. Yeager, C. P. 1996. Feeding ecology of the long-tailed macaque (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia. International Journal of Primatology 17, 51-62.
22. Agetsuma, N. 1995. Dietary selection by Yakushima Macaques (*Macaca fuscata yakui*), the influence of food availability and temperature. International Journal of Primatology 16, 611-627.
23. Agetsuma, N. & Nakagawa, N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: Comparison between Yakushima and Kinkazan. Primates 39, 275-289.
24. Hanya, G. 2004. Diet of a Japanese macaque troop in the coniferous forest of Yakushima. International Journal of Primatology 25, 55-71.
25. Hill, D. A. 1997. Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. American Journal of Primatology 43, 305-322.
26. Astaras, C., Muhlenberg, M. & Waltert, M. 2008. Note on drill (*Mandrillus leucophaeus*) ecology and conservation status in Korup National Park, southwest Cameroon. American Journal of Primatology 70, 306-310.

27. Hoshino, J. 1985. Feeding ecology of Mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. Primates 26, 248-273.
28. Matsuda, I., Tuuga, A. & Higashi, S. 2009. The feeding ecology and activity budget of proboscis monkeys. American Journal of Primatology 71, 478-492.
29. Yeager, C. P. 1989. Feeding ecology of the probiscus monkey (*Nasalis larvatus*). International Journal of Primatology 10, 497-528.
30. Goodall, J. 1986 The Chimpanzees of Gombe. Patterns of Behavior. Cambridge/Massachusetts Belknap Harvard University Press.
31. Post, D. G. 1982. Feeding behavior of Yellow Baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. International Journal of Primatology 3, 403-430.
32. Norton, G. W., Rhine, R. J., Wynn, G. W. & Wynn, R. D. 1987. Baboon Diet, a 5-year study of stability and variability in the plant-feeding and habitat of the yellow Baboons (*Papio cynocephalus*) of Mikumi-National-Park, Tanzania. Folia Primatologica 48, 78-120.
33. Rhine, R. J., Norton, G. W., Wynn, G. W. & Wynn, R. D. 1989. Plant feeding of aellow Baboons (*Papio cynocephalus*) in Mikumi Nation Park, Tanzania, and the relationship between seasonal feeding and immature survival. International Journal of Primatology 10, 319-342.
34. Maisels, F., Gauthierhion, A. & Gautier, J. P. 1994. Diets of 2 sympatric Colobines in Zaire, more evidence on seed-eating in forests on poor soils. International Journal of Primatology 15, 681-701.
35. Marsh, C. W. 1981. Diet Choice among Red Colobus (*Colobus badius rufomitratus*) on the Tana River, Kenya. Folia Primatologica 35, 147-178.
36. Clutten-Brock, T. H. 1975. Feeding behavior of red colobus and black and white colobus in East Africa. Folia Primatologica 23, 165-207.
37. Wich, S. A., Utami-Atmoko, S. S., Setia, T. M., Djoyosudharmo, S. & Geurts, M. L. 2006. Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. International Journal of Primatology 27, 1535-1550.
38. Rodman, P. S. 1977. Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In Primate ecology : studies of feeding and ranging behaviour in lemurs, monkeys, and apes. (ed. T. H. Clutten-Brock). London, New York: Academic Press.
39. Galdikas, B. M. F. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. International Journal of Primatology 9, 1-35.
40. Mitchell, A. H. 1994. Ecology of Hose's langur, *Presbytis hosei*, in mixed logged and unlogged dipterocarp forest of northeast Borneo. New Haven: Yale University.
41. Sangchantr, S. 2004. Social organization and ecology of mentawai leaf monkeys (*Presbytis potenziani*): Colombia University.

42. Davies, A. G., Bennett, E. L. & Waterman, P. G. 1988. Food selection by 2 Southeast Asian Colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. Biological Journal of the Linnean Society 34, 33-56.
43. Davies, G. 1991. Seed-Eating by Red Leaf Monkeys (*Presbytis rubicunda*) in dipterocarp forest of Northern Borneo. International Journal of Primatology 12, 119-144.
44. Li, Y. M. 2006. Seasonal variation of diet and food availability in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. American Journal of Primatology 68, 217-233.
45. Hladik, C. M. 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes. (ed. T. H. Clutten-Brock), pp. 323-353. London: Academic Press.
46. Stanford, C. B. 1991. The diet of the capped langur (*Presbytis pileata*) in a moist deciduous forest in Bangladesh. International Journal of Primatology 12, 199-216.
47. Solanki, G. S., Kumar, A. & Sharma, B. K. 2008. Feeding ecology of *Trachypithecus pileatus* in India. International Journal of Primatology 29, 173-182.
48. Dela, J. D. S. 2007. Seasonal food use strategies of *Semnopithecus vetulus nestor*, at Panadura and Piliyandala, Sri Lanka. International Journal of Primatology 28, 607-626.
49. Isler, K., Kirk, E. C., Miller, J. M. A., Albrecht, G. A., Gelvin, B.R. & Martin, R.D. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. Journal of Human Evolution 55, 967-978.
50. Wich, S. A. & Nunn, C. L. 2002. Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. Behavioral Ecology and Sociobiology 52, 474-484.
51. Lindenfors, P. & Tullberg, B.S. 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. Biological Journal of the Linnean Society. 64(4): p. 413-447.
52. Smith, R.J. & Jungers, W.L. 1997. Body mass in comparative primatology. Journal of Human Evolution 32, 523-559.
53. Gordon, A.D. 2006. Scaling of size and dimorphism in primates II: Macroevolution. International Journal of Primatology 27, 63-105.
54. Setchell, J.M., Lee, P. C., Wickings, E. J. & Dixson, A. F. 2001. Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). American Journal of Physical Anthropology 115, 349-360.
55. Ross, C. 2003. Life history, infant care strategies, and brain size in primates, in Primate life histories and socioecology, P. Kappeler and M.E. Pereira, Editors. Cambridge University Press: Cambridge. p. 266–284.

56. Bourliére, F., Hunkeler, C. & Bertrand, C. 1970. Ecology and behaviour of Lowe's guenon (*Cercopithecus campbelli, lowei*) in the Ivory Coast, in Old World monkeys, J.R. Napier and P.H. Napier, Editors. Academic Press: New York. p. 297-350.
57. Pazol, K., Carlson, A.A., & Ziegler, T.E. 2002. Female reproductive endocrinology in wild blue monkeys: a preliminary assessment and discussion of potential adaptive functions, in The Guenons: diversity and adaptation in African monkeys, M.E. Glenn and M. Cords, Editors. Kluwer Academic/Plenum Publishers: New York. p. 217-232.
58. Harris, T.R. & Monfort, S.L. 2006. Mating behavior and endocrine profiles of wild black and white Colobus monkeys (*Colobus guereza*): Toward an understanding of their life history and mating system. American Journal of Primatology 68, 383-396.
59. Lee, P.C. 1999. Comparative primate socioecology. Cambridge: University Press.
60. Thierry, B. 2007. The macaques: a double-layered social organization, in Primates and Perspective, C.J. Campbell, et al., Editors. Oxford University Press: Oxford. p. 224-339.
61. Fashing, P.J. 2007. African colobine monkeys: patterns of between-group interaction, in Primates in Perspective, C.J. Campbell, et al., Editors. Oxford University Press: Oxford.
62. Markham, R. 1990. Doing it naturally: reproduction in captive orangutans (*Pongo pygmaeus*), in The Neglected Ape, R.D. Nadler, et al., Editors. Plenum Press: London. p. 273-278.
63. van Woerden, J. T., van Schaik, C. P. & Isler, K. 2010. Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. American Naturalist 176, 758-767.
64. Healy, S.D. & Rowe, C. 2007. A critique of comparative studies of brain size. Proceedings of the Royal Society B-Biological Sciences 274(1609): p. 453-464.
65. Hladik, C.M., Chivers, D.J. & Pasquet, P. 1999. On diet and gut size in non-human primates and humans: Is there a relationship to brain size? Discussion and criticism. Current Anthropology 40, 695-697.
66. Fish, J.L. & Lockwood, C.A. 2003. Dietary constraints on encephalization in primates. American Journal of Physical Anthropology 20, 171-181.
67. Dunbar, R.I.M. 1992. Neocortex size as a constraint on group size in primates. Journal of Human Evolution 22, 469-493.
68. Clutton-Brock, T.H. & Harvey, P.H. 1980. Primates, Brains and Ecology. Journal of Zoology 190, 309-323.
69. Hemingway, C.A. & Bynum, N. 2005. The Influence of Seasonality on Primate Diet and Ranging, in Seasonality in Primates, D.A. Brockman and C.P. van Schaik, Editors. Cambridge University Press: New York. p. 57-104.
70. Shultz, S. & Dunbar, R.I.M. 2007. The evolution of the social brain: anthropoid primates contrast with other vertebrates. Proceedings of the Royal Society B-Biological Sciences. 274, 2429-2436.

71. Martin, R.D. 1996. Scaling of the mammalian brain: The maternal energy hypothesis. News in Physiological Sciences 11, 149-15672.

72. Dunsworth, H., Pontzer, H. & Deacon, T. 2011. Energetics, not pelvic constraints, determine human gestation length and altriciality. American Journal of Physical Anthropology 144, 129-129.

Chapter 4.

What Enables Cognitive Buffering in Primates?

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Abstract

Seasonal availability of food resources can promote encephalization as predicted by the Cognitive Buffer hypothesis, but starvation periods due to seasonality also pose an energetic constraint on brain brain size evolution. We show that in all taxonomic groups, relatively large-brained primates buffer the seasonality of their environment cognitively, but the magnitude of the effect varies between the groups. Here, we aim to identify factors that facilitated or hindered the presence of cognitive buffering in primates. As expected, buffering is facilitated by habitat seasonality, up to a certain degree. Body mass, group size or life history pace do not correlate with cognitive buffering, but largely folivorous primates buffer less than frugi/omnivorous primates, even if their overall smaller brain size is taken into account. Our results emphasize the importance of ecological constraints on brain size evolution.

Introduction

The Cognitive Buffer hypothesis states that the main selective advantage of having a brain that is large relative to body mass is to deal better with novel or varying ecological conditions (Allmann et al. 1993; Deaner et al. 2003; Sol 2009). Thus, variation in encephalization among species is explained by the fitness benefits of increased cognitive abilities (Figure 4.1). Several studies in birds have supported this hypothesis. Indeed, relatively larger-brained birds, but also mammals, are better at establishing themselves in new environments than smaller-brained ones (Shultz et al. 2005; Sol et al. 2005a; Sol et al. 2008). Also, Neotropical parrots living in more seasonal habitats have relatively larger brains than those living in climatically less seasonal habitats (Schuck-Paim et al. 2008). However, studies in other taxa did not find support for the Cognitive Buffer hypothesis. First, in fish, establishment success in new environments is not associated with brain size, but rather with fecundity and parental investment (Drake 2007). Second, lemurs living in more seasonal habitats have relatively *smaller* rather than larger brains (van Woerden et al. 2010). The absence of a cognitive buffer effect in these groups may be due to a predominance of the high energetic costs of brain tissue (Mink et al. 1981).

Regarding seasonality, the Expensive Brain framework (Isler and van Schaik 2009a) predicts that the evolution of relative large brains is constrained by the high costs of growing and maintaining the brain during the periods of food scarcity which occur in highly seasonal habitats (Figure 4.1). This hypothesis thus seemingly contrasts with the Cognitive Buffer hypothesis. However, energetic constraints and cognitive buffer effects are not mutually exclusive, because the two processes operate simultaneously. Either one may predominate, resulting in an overall positive correlation between seasonality and brain size if cognitive buffering prevails, an overall negative correlation if energetic costs prevail, or no correlation at all if these effects cancel each other out. An example of the latter case may be found in catarrhine primates. Reader and MacDonald (2003) found no correlation between climatic variability and either relative brain size or behavioral flexibility in African anthropoid primates, which they interpreted as an absence of cognitive buffering in this group. But recently, we demonstrated that both cognitive buffering and energetic constraints on brain size exist in catarrhine primates, leading to the absence of a correlation between seasonality and brain size (van Woerden et al. 2011). In order to show this, the amount of cognitive buffering must be measured directly by looking at the difference between the seasonality of the environment and the seasonality experienced by the animal, as measured by

the variability in energy intake over a year (van Woerden et al. 2010, 2011). This approach allows for the identification of presence or absence of both energetic constraints of seasonality on brain size and cognitive buffer effects in a clade, depending on the availability of detailed data on diet or field metabolic rates.

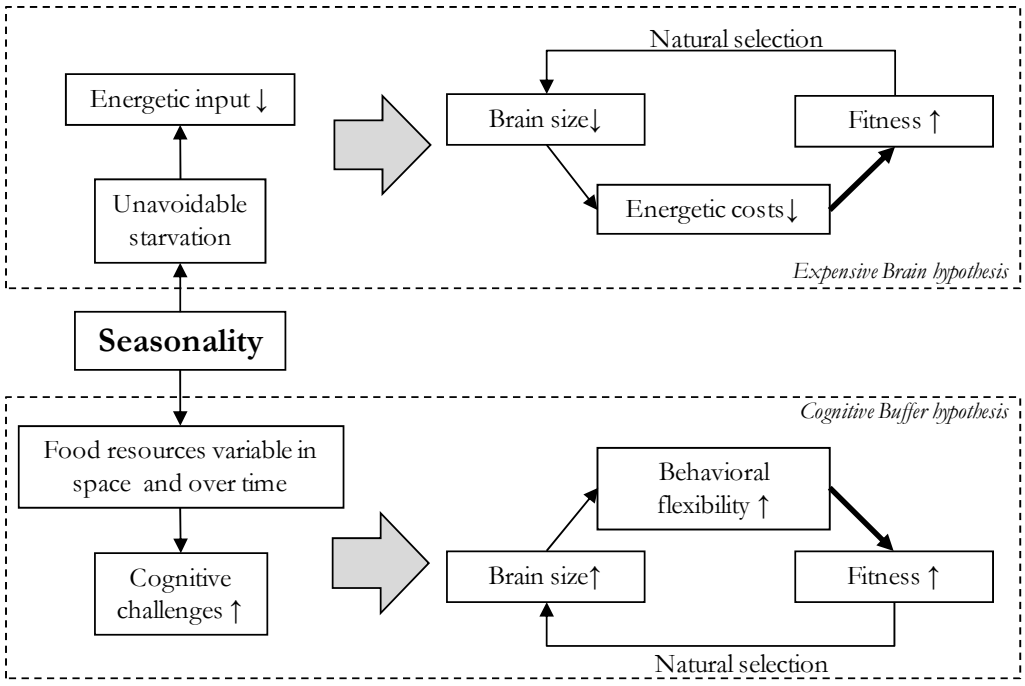

Figure 4.1. Effects of seasonality on brain size evolution. The Cognitive Buffering hypothesis and the Expensive Brain framework are alternative, but not mutually exclusive pathways.

Our previous finding of a very weak cognitive buffer effect in lemurs (van Woerden et al. 2010), in combination with conflicting reports from other taxa (Drake 2007, Reader and MacDonald 2003, van Woerden et al. 2010, 2011), suggests that cognitive buffering is not ubiquitous. This raises the question why cognitive buffering is found in some clades, but not others. Potential factors that facilitate cognitive buffering or increase its fitness benefits are listed in Table 4.1. These can be grouped into three main categories. The first is habitat seasonality itself; a very stable food supply throughout the year does not require any buffering at all. The second category is related to the dietary niche of a species. If the options to switch to other food types are very restricted by aspects of habitat use (small home range or a completely arboreal

lifestyle) or a specialized morphology (e.g. folivory), cognitive buffering is less likely to occur. The third category is related to life-history pace or life style: cognitive buffering does not yield much survival benefit in short-lived, highly fertile animals that suffer high unavoidable mortality. At the same time, living in social groups may increase the opportunities for social learning and thus increase the survival benefits of enhanced cognitive abilities. When we test which of these factors facilitate or hinder cognitive buffering, we must control for the fact that cognitive buffering is positively correlated with relative brain size, because otherwise we might find significant correlations only because they reflect a relationship between overall cognitive abilities and these factors. Thus, we must control for relative brain size in all these tests.

In order to investigate which of these variables correlate with cognitive buffering, we first examine cognitive buffering and energetic constraints on brain size in a third clade of primates, the platyrrhines of the New World, which are the sister group of the catarrhine primates (Old World monkeys and apes). In the combined primate sample, we then test which factors correlate with the amount of cognitive buffering (Table 4.1).

Table 4.1. Potential factors that facilitate or hinder cognitive buffering in primates.

Pathway	Factor	Reasoning	Prediction
Habitat	Habitat seasonality	If the food supply is very stable over time, buffering is not necessary.	Cognitive buffering is positively correlated to the degree of habitat seasonality.
Dietary switching options	Folivory	Folivores have fewer options to change their diet than species with a broader diet (most frugivores and omnivores).	Folivores show less cognitive buffering than non-folivores.
	Home range size	Larger home ranges contain more different food sources to exploit.	Cognitive buffering is positively correlated to home range size.
	Terrestriality	Spending time on the ground opens up more diverse food sources.	Cognitive buffering is positively correlated with the occurrence of terrestriality.
Life history and life style	Body size	Smaller animals have a faster life history pace, and suffer a higher predation risk, which results in high unavoidable mortality rates. Survival through cognitive buffering therefore is less beneficial in small animals.	Cognitive buffering is positively correlated with body mass.
	Age of first reproduction (AFR)	Animals with slow life-histories would benefit most from cognitive buffering	Cognitive buffering is positively correlated with AFR.
	Group size	Living in groups increases opportunities for social learning and cognitive buffering is more likely to enhance fitness.	Cognitive buffering and group size are positively correlated

Methods

Brain size relative to body mass

As a measure of adult female brain sizes we measured endocranial volumes (ECV) using glass beads from skulls with a known origin from several museums in Europe and USA. In order to control for body mass, female body masses from wild study populations were taken from literature sources, or if possible taken from the same museum specimens that the ECV was measured from (Table A4.1).

Seasonality measures

To estimate how much seasonality was experienced by the primates, we calculated the coefficient of variation (CV = standard deviation / mean) over monthly means of dietary item intake multiplied by their energetic quality (8 for insects, 5 for fruits, seeds and flowers, 3 for gum and young leaves, 1 for mature leaves, as calculated from g crude fiber/kg dry matter by Langer 2003). Data were acquired from literature sources reporting monthly dietary intake of ≥12 consecutive months. In total experienced seasonality (XPR), i.e. CV in diet, was available for 23 platyrrhines, 36 catarrhines and 19 lemurs (Table A4.1).

As a measure for the seasonality in the environment (ENV) we extracted the coefficient of variation (CV) in Normalized Vegetation Index, NDVI, (e.g. Pettorelli et al. 2005) from the GIMMS database (Tucker et al. 2005). NDVI is a more direct measure of plant productivity and thus a better proxy for food availability than rainfall. The amount of cognitive buffering was then calculated as the difference between environmental and experienced seasonality (ENV-XPR). Animals that buffer more, keep their energy intake (experienced seasonality = XPR) more constant than expected based on variation in their habitat (environmental seasonality = ENV), and therefore will have a large difference between ENV and XPR. To calculate this difference we subtracted CV in diet from CV in plant productivity (Normalized Difference Vegetation Index, NDVI).

To estimate habitat seasonality we additionally extracted minimal temperature from the WorldClim data base (Hijmans et al. 2005) using ArcGIS 9.1, as a complementary proxy of food availability for those primates living in extreme habitats, e.g. *Macaca fuscata* or *Rhinopithecus ssp*.

Analyses

All analyses were preformed in R (R-Development-Core-Team 2010), controlling for phylogenetic relatedness with the caper package (Orme 2011). The phylogeny was based on version 2 of 10Ktrees (Arnold et al. 2010, see Figure A4.1). All continuous variables were log-transformed before analyses to increase normality. The influence of potentially confounding variables was ruled out in catarrhine and strepsirrhine primates (van Woerden et al. 2010, 2011), and the effects on the results are minor also in platyrrhine primates, although a reduction of the sample size due to lack of data adds unstability to the analyses (data not shown).

In order to test which factors facilitate cognitive buffering in primates, we selected the best-fit model out of the following variables: environmental seasonality (CV in NDVI), minimal temperature (<15˚C or >15˚C), folivory (folivorous or non-folivorous), home range size, terrestriality (terrestrial, partly terrestrial or arboreal), female body mass, age of first reproduction, group size, and residuals of female brain size vs. female body mass. We also tested the effect of all of the above variables on cognitive buffering separately, but still controlling for relative brain size.

Results

First, we tested whether three major phylogenetic clades of primates (platyrrhines, catarrhines and lemurs) exhibit cognitive buffering or energetic constrains of seasonality on relative brain size. All primates that experienced more seasonality in their energy intake had relatively smaller brains (Figure 4.1 and Table 4.2), indicating an energetic constraint on relative brain size in all groups. In both platyrrhine and catarrhine primates we found a significant positive relationship between the amount of cognitive buffering and the relative size of their brains. In these two groups, the cognitive buffering and the energetic constraints were equally strong, resulting in the absence of a clear correlation between relative brain size and environmental seasonality. Conversely, a cognitive buffering effect was only weakly expressed in lemurs, and thus the correlation between environmental seasonality and relative brain size was significantly negative in this group. In the combined primate sample, both energetic constraints and cognitive buffer effects were very strong, leaving no overall relationship between environmental seasonality and brain size (Table 4.2).

Second, to see which factors could best predict the occurrence of cognitive buffering in the combined primate sample, we tested each of them individually (Table 4.3a). After controlling for relative brain size, only environmental seasonality and folivory were significantly correlated with cognitive buffering. These same factors entered into the best-fit model (Table 4.3b). The weak trends of body mass and group size with cognitive buffering disappeared once folivory was included in the model, but minimal temperature remained as a negative trend (see Table A4.2).

Table 4.2. Phylogenetic least squares regressions (PGLS) testing for possible effects of seasonality on brain size in 78 nonhuman primates. Relationships are shown between brain size and (a) seasonal variation in diet, i.e. seasonality as experienced by the primates, (b) environmental variation relative to diet variation, i.e. cognitive buffering, and (c) environmental seasonality, controlling for body mass. All lambdas were close to 1 (>0.99), which indicates that there was a strong phylogenetic signal in the data and the necessity of applying a phylogenetic method (Pagel 1999).

		Estimate	**Std. Error**	**t-value**	***P***
A) Energetic constraints	Body mass	0.70	0.03	22.7	<0.0001
	CV in diet (XPR)	-1.24	0.27	-4.6	<0.0001
B) Cognitive buffering	Body mass	0.69	0.03	22.0	<0.0001
	[ENV-XPR]	0.83	0.18	4.6	<0.0001
C) Environmental seasonality	Body mass	0.67	0.04	18.5	<0.0001
	CV plant productivity (ENV)	-0.01	0.12	-1.1	0.2761

Table 4.3. Phylogenetic least squared regressions (PGLS) with cognitive buffering as the response variable and each possible explanatory variable separately (a), controlling for relative brain size in each analysis, and the eventual best fit model from all these variables (b).

(a) Individual factors vs cognitive buffering

Variable	N	est. lambda (λ)	Estimate	Std. Error	t-value	*P*
Environmental seasonality	78	0.73	0.308	0.145	**2.13**	**0.04**
Residual Brain size			0.222	0.041	**5.40**	**<0.0001**
Minimal temperature	78	0	0.025	0.019	1.34	0.19
Residual Brain size			0.141	0.024	**5.87**	**<0.0001**
Folivory	78	0	-0.067	0.019	**-3.62**	**0.0005**
Residual Brain size			0.12	0.023	**5.16**	**<0.0001**
Home range	51	0	<-0.001	0.008	-0.05	0.96
Residual Brain size			0.135	0.04	**3.34**	**0.0016**
Terrestriality	78	0	0.021	0.018	1.17	0.25
Residual Brain size			0.145	0.024	**6.16**	**<0.0001**
Body mass	78	0	-0.011	0.008	-1.51	0.14
Residual Brain size			0.165	0.026	**6.37**	**<0.0001**
Age first reproduction	59	0	-0.023	0.023	-1.01	0.31
Residual Brain size			0.174	0.336	**5.16**	**<0.0001**
Group size	74	0	0.018	0.012	1.51	0.14
Residual Brain size			0.141	0.025	**5.60**	**<0.0001**

(b) Best-fit model

Variable	N	est. lambda (λ)	Estimate	Std. Error	t-value	*P*
Environmental seasonality	78	0	0.344	0.140	**2.46**	**0.016**
Minimal temperature			0.029	0.017	1.70	0.09
Folivory			-0.073	0.018	**-4.03**	**0.0001**
Residual Brain size			0.113	0.023	**4.96**	**<0.0001**

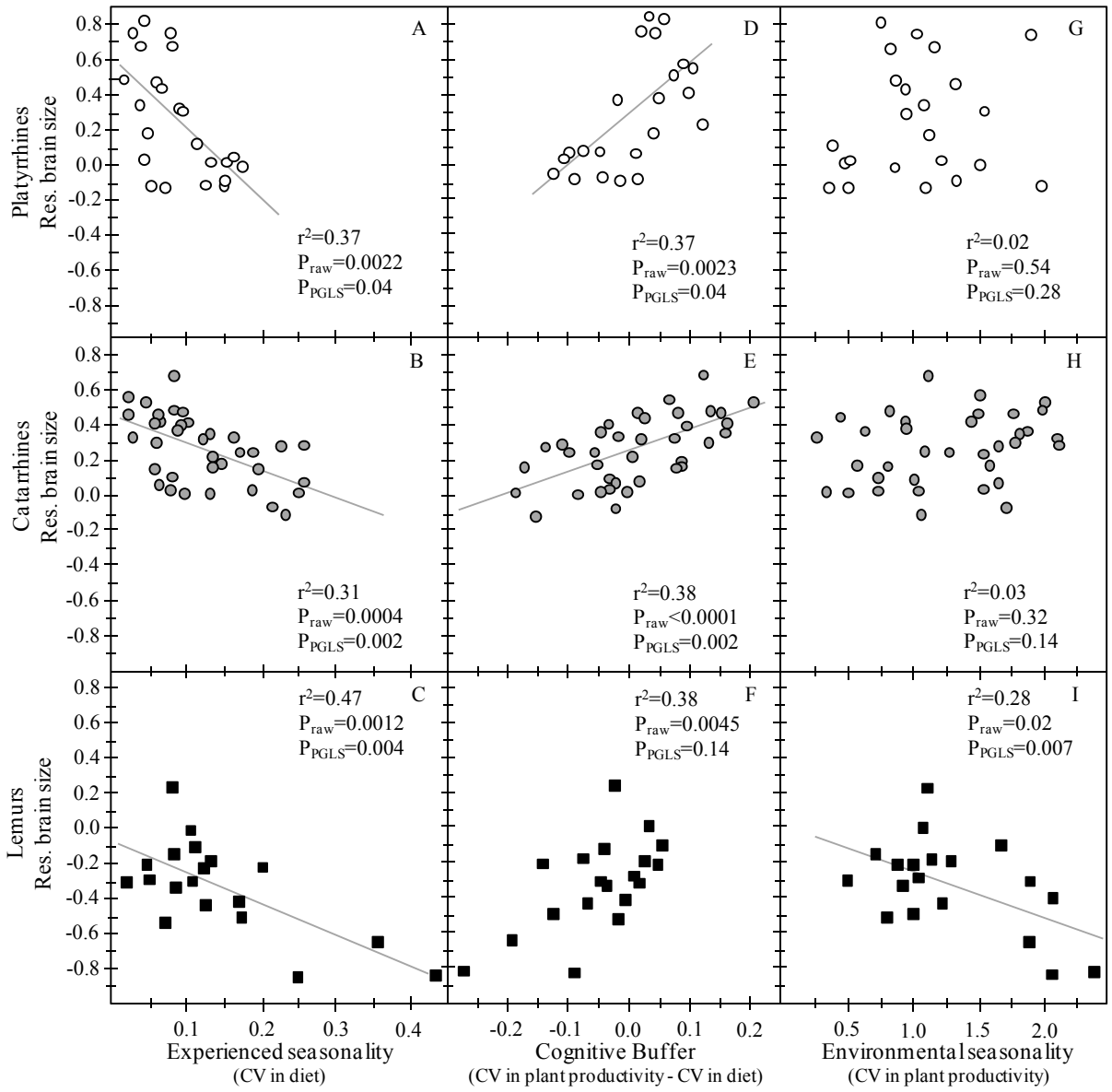

Figure 4.1. Correlations between seasonality and relative brain size in three primate clades. Data points represent species means. P-values based on species-level (P_{raw}) and phylogenetic least square regressions (P_{PGLS}). Note that in lemurs (F), a cognitive buffer effect was not confirmed by phylogenetic analyses.

Discussion

Complementing earlier analyses on lemurs and catarrhine primates, in this paper we first tested whether energetic constraints and cognitive buffering also occur in platyrrhine primates. Our results showed that energetic constraints through seasonality play a role in all primate lineages, as brain size is negatively correlated with the extent of fluctuations in energy intake, and thus experienced seasonality. Cognitive buffering, i.e. reducing the fluctuations of energy intake relative to habitat seasonality, occurred in platyrrhines, just as we had found before in catarrhines (van Woerden et al. 2011), and thus in haplorhines generally, but to a lesser degree in lemurs. Haplorhines that could keep their energy intake more constant throughout the year despite high variation in food availability (as proxied by habitat seasonality) had relatively larger brains. Nonetheless, from these correlations we cannot determine causality; it therefore remains an open question whether relatively larger brains (and their associated enhanced cognitive capacities, e.g. Deaner et al. 2007; Reader et al. 2011) are a cause or a consequence of cognitively buffering seasonality.

Our main objective was to identify the conditions that facilitate or hinder cognitive buffering in primates, controlling for the effect of overall cognitive abilities (proxied by brain size relative to body mass). As expected, we found that cognitive buffering is positively correlated with the overall seasonality of the environment. However, in extremely seasonal, non-tropical environments we would not expect to see much cognitive buffering in frugivores, granivores or insectivores, as the complete absence of these food sources during lean periods necessitates other survival strategies such as fat storage in combination with hibernation. Despite very small sample sizes, because only a few nonhuman primates inhabit such extreme habitats, we did indeed find a positive trend of very low minimal temperatures on cognitive buffering in the best-fit model. This suggests that non-carnivorous animals living in temperate or arctic climates face a stronger constraint than their tropical counterparts on the extent of cognitive buffering of habitat seasonality.

The second factor identified in our best-fit model, folivory, was negatively correlated with the amount of cognitive buffering. Note that in this model, relative brain size was included as a covariate, and the negative correlation could therefore not be due to the well-known fact that folivorous primates are relatively smaller-brained than frugivorous primates (Clutton-Brock and Harvey 1980). Primates relying on more folivorous diets, generally have special digestive and

dental adaptations (Langer 1988; Vogel et al. 2008), which allow them to rely on foods with more fiber, fewer readily available calories or higher levels of antifeedants. Even though folivorous primates also suffer from food scarcity in seasonal habitats (Harris et al. 2010), their food sources during lean periods are generally staple fallback foods (Marshall and Wrangham 2007) which do not require cognitive skills to find or to feed on. Primates without these special folivorous adaptations usually rely on filler fallback foods during lean periods (Marshall and Wrangham 2007). These can be foods of higher energetic content which have a more patchy distribution and may even need extractive foraging or tool use to eat, such as palm nuts in brown capuchins (Terborgh 1983) and oil-palm nut in chimpanzees (Yamakoshi 1998). Tool use and extractive foraging are probably the energetically most rewarding behaviors used to cognitively buffer environmental conditions, since they provide access to hidden and highly nutritional food items.

To assess folivory, we used a dichotomous variable indicating more or less than 50% of leaves in the overall diet. This measure is more appropriate to test whether largely folivorous species are applying cognitive buffering than a continuous measure such as the percentage of leaves in the overall diet. The latter would induce a circularity problem, as measuring the amount of cognitive buffering of a species is by necessity negatively correlated to the amount of leaves in the overall diet, because in primates food sources during the lean period largely consist of leaves. Thus, eating slightly more poor-quality fallback foods increases the overall percentage of leaves in the diet, and simultaneously reduces the difference between environmental and experienced seasonality, our measure of cognitive buffering. The dichotomous variable, on the other hand, represents only a few, pronounced contrasts between largely folivorous and largely frugivorous taxa and is thus not by definition correlated with the amount of cognitive buffering.

Although we identified two factors related to cognitive buffering (folivory and environmental seasonality), they fail to explain why cognitive buffering is weak or absent in lemurs. This finding could be explained by some measurement error of dietary intake in small or nocturnal primates, which in combination with the rather small sample size could affect the stability of a phylogenetic analysis (cf. Martin et al. 2005). But as lemurs exhibit a variety of physiological buffers to cope with their highly seasonal habitat, the absence of cognitive buffering in this group (with the remarkable exception of the aye-aye, *Daubentonia madagascariensis*) can also reflect the trade-off between physiological and cognitive buffering recently demonstrated in other mammals (Navarrete et al. ms). It may be that cognitive buffering

is less feasible for lemurs because they use a large proportion of their metabolism for the brain. Relative costs of brain growth and maintenance are high in animals that are small, relatively large-brained (Mink et al. 1981), and hypometabolic, all of which is the case in lemurs. It would be interesting to see whether the percentage of metabolism spent on brain maintenance is negatively correlated with cognitive buffering. However, since metabolic rates are available for only eight primate species in our sample, we were not able to test this prediction. If we assume that lemurs pay relatively more for their brains than haplorhines, cognitive buffering would need to overcome an even more severe energetic barrier to be of any benefit. This may be the reason for a different strategy in many members of this group.

We predict that cognitive buffering is found in all mammalian clades that live in moderate to highly seasonal habitats and are not specialized folivores or herbivores. However, energetic constraints also apply and may hide the cognitive buffer effects, leading to a negative correlation between habitat seasonality and relative brain size. The only animal groups where cognitive buffering prevails, producing a positive correlation between habitat seasonality and brain size, are probably those where habitat seasonality is not a good proxy of food availability since their food source is not reflecting climatic fluctuations (e.g. carnivores), or those that can easily move to other habitats, such as birds or cetaceans (Sol et al. 2007; Schuck-Paim et al. 2008).

In conclusion, we have shown that ecological factors explain much of the variation in primate brain size. Seasonality is both cognitively challenging and energetically expensive. The key to identify the balance of these processes is to obtain direct estimates of both the experienced seasonality and the extent of cognitive buffering. All primates suffer from the energetic consequences of seasonal habitats, but only those that can benefit from a varied diet have the opportunity to benefit from the cognitive challenges.

Acknowledgements

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Appendix Chapter 4

Table A4.1. Data used in this study.

Species	BoM (g)	ECV (ml)	CV in diet	Study Location for diet	Buffer (Diff NDVI[†])	CV in NDVI[‡]	Foli-vore	HR (ha)[(1)]	Group size[§]	Terres triality	AFR
Alouatta caraya	4468[*]	49.2	0.153	El Piñalito Provincial Park (2); Brasilera Island, Argentina (3)	-0.100	0.151	1		8	3	3.7
Alouatta guariba	4550[*]	48.5	0.176	El Piñalito Provincial Park (2); Santa Genebra Reserve, São Paulo, Brazil (4, 5)	-0.106	0.087	1		7.4	3	
Alouatta palliata	5350[*]	50.4	0.152	La Selva, Heredia, Costa Rica (6); Los Tuxtlas, Veracruz, Mexico (7)	-0.125	0.133	1	43.5	12	3	4
Alouatta seniculus	5600[*]	55.8	0.162	Nouragues Station, French Guiana (8)	-0.047	0.122	1	12.1	4.6	3	5.2
Ateles belzebuth	8484[*]	112.8	0.066	Maracá, Roraima, Brazil (9); Proyecto Primates Research site, Yasuní Nat. Park, Ecuador (10)	0.073	0.091	0	441.0	12.5	3	
Ateles chamek	9330[(11)]	109.8	0.087	Noel Kempff Mercado National Park (12)	-0.022	0.096	0		11.5	3	
Ateles paniscus	8440[(13)]	107.6	0.033	Raleighvallen-Voltzberg Nature Reserve, Surinam (14)	0.098	0.107	0	206.0	18	3	5
Brachyteles arachnoides	8500[(11)]	102.2	0.089	Fazenda Montes Claros, Minas Gerais, Brazil (15); PECB, Sao Paulo, Brazil (16); Barreiro Rico, São Paulo, Brazil (17)	0.043	0.154	0	294.7	26	3	9.1
Cacajao calvus	2880[(18)]	71.9	0.037	Lake Teiú, Amazonas, Brazil (19)	0.023	0.083	0	500.0	17.5	3	3.6
Callicebus personatus	1002[¥]	18.2[¥]	0.042	Estacão Experimental Lemos Maia, Brazil (20)	0.010		0	4.7	3.7	3	5
Callimico goeldii	485	11.1[§]	0.129	San Sebastian, Pondo, Bolivia (21)	-0.080		0	42.5	5	3	1.5
Callithrix aurita	360[¥]	10.1	0.113	Fazenda Lagoa, Minas Gerais, Brazil (22); Espíríto Santo, Brazil (23)	0.039	0.038	0		8.3	3	
Callithrix jacchus	322[(24)]	7.4	0.149	National Forestry Station (FLONA), Nísia Floresta, Brazil (25)	-0.045	0.198	0	13.3	8.9	3	1.7
Cebus apella	2501[*]	64.2	0.078	Nouragues Station, French Guiana (26)	0.038	0.116	0	344.0	11	3	6.7
Cebus capucinus	2437[*]	69.3	0.076	Lomas Barbudal Biological Reserve, Guanacaste, Costa Rica (27)	0.031	0.103	0	86.3	15	3	6
Cebus nigritus	2215[*]	64.1	0.026	Santa Genebra Reserve, São Paulo, Brazil (28)	0.060	0.188	0		16.5	3	
Cebus olivaceus	2202[*]	69.6	0.044	Fundo Pecuario Masaguaral, Venezuela (29)	0.028	0.075	0	257.0	20	3	6
Chiropotes chiropotes	2580[(18)]	55.1	0.013	Proyecto de Primatología Ecológica de Guayana, Venezuela (30)	0.089	0.087	0	300.0	17	3	3
Lagothrix lagotricha	7020[(11)]	90.3	0.055	Yasuní Nat. Park, Ecuador (31)	0.101	0.130	0	544.8	33	3	9
Pithecia pithecia	1816[*]	31.6	0.044	Guri Lake (Pithecia Isl), Venezuela (32)	0.119	0.113	0	290	2.6	3	2.1

Saguinus bicolor	473[¥]	9.5[¥]	0.125[±]	Manaus (suburb), Amazonas, Brazil (33)	-0.089		0		5.2	3	
Saguinus fuscicollis	412[(34)]	8.6	0.070	upper Urucu river, Amazonas, Brazil (35); San Sebastian, Pondo, Bolivia (21)	-0.013	0.109	0	34.3	6	3	1.9
Saguinus mystax	538[*]	10.4	0.050	upper Urucu river, Amazonas, Brazil (35)	0.016	0.051	0	32.3	5.3	3	1.3
Bunopithecus hoolock[(36)]	6350	106.6	0.045	Lawachara, Bangladesh	0.206	0.201	0	24.2	3.5	3	7
Cercopithecus ascanius[(36)]	2902	56.7	0.102	Budongo Forest, Uganda; Kakamega, Kenya	-0.04	0.095	0	31.2	22	3	5
Cercopithecus campbelli[(36)]	2545	54.9	0.064	Tai Forest, Cote d'Ivoire	0.078	0.175	0	21.5	9	3	3.5
Cercopithecus cephus[(36)]	2880	60.7	0.083	Makokou; Lope Reserve, Gabon	0.133	0.198	0	34	6	3	5
Cercopithecus diana[(36)]	3900	57.3	0.136	Tai Forest, Cote d'Ivoire	0.006	0.154	0	105.5	24	3	5.4
Cercopithecus mitis[(36)]	4629	65.8	0.188	Zomba plateau, Malawi; Budongo Forest, Uganda; Kakamega, Kenya	-0.1	0.127	0	83.8	27	3	5.4
Cercopithecus nictitans[(36)]	4260	66.8	0.122	Makokou; Makande; Lope Reserve, Gabon	0.073	0.209	0	120.5	13.5	3	5
Cercopithecus petaurista[(36)]	2919	52.7	0.163	Tai Forest, Cote d'Ivoire	-0.02	0.180	0		10	3	
Cercopithecus pogonias[(36)]	2900	56.5	0.06	Makokou; Makande, Gabon	0.160	0.144	0	103	14	3	5
Cercopithecus stuhlmanni[(36)]	4629	65.8	0.172	Budongo, Uganda	-0.06	0.108	0		~27	3	
Colobus angolensis[(36)]	7849	65.8	0.233	Nyungwe forest, Rwanda	-0.15	0.107	1		>300	3	3
Colobus guereza[(36)]	7503	72.6	0.25	Kakamega, Kenya; Budongo Forest, Uganda	-0.19	0.106	1	12.6	8	3	4.8
Colobus polykomos[(36)]	6708	71.0	0.259	Tai Forest, Cote d'Ivoire; Tiwai Island, Sierra Leone	-0.02	0.165	1	36	13.6	3	5.5
Gorilla gorilla[(36)]	71500	434.4	0.257	Bai Hokou; Mondika, CAR;Nouabale-Ndoke reserve, Congo	-0.11	0.211	1	2545	9	2	10.2
Hylobates lar[(36)]	5383	100.1	0.025	Ketambe, Indonesia	0.068	0.152	0	34.2	5	3	10
Lophocebus albigena[(36)]	5976	90.7	0.095	Dja Reserve, Cameroon; Makande, Gabon	0.096	0.096	0		15	2	6
Macaca fascicularis[(36)]	3516	61.0	0.130	Kutai National Reserve; Ketambe; Tanjung Puting, Indonesia	-0.05	0.064	0	69.3	27	3	5.2
Macaca fuscata[(36)]	8030	97.9	0.227	Yakushima, Japan	-0.14	0.164	0	177.1	12	2	6.1
Macaca nigra[(36)]	5470	80.2	0.028	Tangkoko-Dua Sudara Nature Reserve	0.017	0.026	0	260	67	2	5.4
Mandrillus leucophaeus[(36)]	8840	126.3	0.025	Korup Nat Park, Cameroon	0.149	0.149	0		77	1	5
Mandrillus sphinx[(36)]	12800	137.3	0.060	Mvini village, Cameroon	0.130	0.178	0		95	1	5
Nasalis larvatus[(36)]	9730	84.9	0.134	Menanggul River; Tanjung Puting, Indonesia	-0.09	0.052	1	261	12.7	3	4.5
Pan t. schweinfurthii[(36)]	33700	391.6	0.083	Gombe, Uganda	0.119	0.113	0	1787	44	2	13.3

Papio cynocephalus[36]	13121	149.6	0.091	Amboseli National Park, Kenya; Mikumi National Park, Tanzania	0.156	0.185	0	4564	56	1	6
Piliocolobus badius[36]	7130	63.7	0.214	Tai Forest, Cote d'Ivoire; Botsima; Mchelelo, Kenya; Gombe, Tanzania; Tiwai Island, Sierra Leone	-0.02	0.170	1		34.3	3	
Pongo abelii[36]	41151	349.7	0.065	Ketambe, Indonesia	0.028	0.046	0		1.5	3	15.4
Pongo p. wurmbii[36]	36754	334.6	0.095	Gunung Palung; Tanjung Putting; Tuanan, Indonesia	0.012	0.083	0	2250	1	3	15.7
Presbytis hosei[36]	5630	60.0	0.082	Off the Semaga river, Indonesia	-0.05	0.074	1		5.5	3	4
Presbytis potenziani[36]	4817	57.0	0.068	Muntei, N Pagi Isl, Indonesia	0.013	0.102	1	22	6	3	
Presbytis rubicunda[36]	6223	68.8	0.081	Sepilok Virgin Jungle Reserve, Malaysia	-0.03	0.075	1	64.4	6	3	
Presbytis thomasi[36]	6350	64.7	0.100	Ketambe, Indonesia	-0.01	0.035	1	37.7	8	3	5.4
Procolobus verus[36]	3707	51.6	0.058	Tai Forest, Cote d'Ivoire	0.084	0.160	1	26.5	7.8	3	3.5
Rhinopithecus roxellana[36]	11600	114.3	0.146	Qianjiaping, Hubei prov, China	0.085	0.315	1		120	3	
Semnopithecus priam[36]	6575	75.3	0.199	Polonnaruwa, Sri Lanksa	-0.17	0.080	1		~9	2	6.7
Trachypithecus pileatus[36]	11340	97.3	0.189	Madhupur Nat Park, Bangladesh; Pakhui Wildlife Sanctuary, India	-0.03	0.154	1	42.5	9	3	
Trachypithecus vetulus[36]	7459	83.7	0.138	Polonnaruwa; Panadura, Sri Lanka	-0.05	0.059	1	4.4	13	3	4
Avahi occidentalis[37]	801	7.92	0.357	Ampijoroa	-0.196	19.0	1	1.9	5	3	2.6
Cheirogaleus medius[37]	139	2.53	0.250	Kirindy	-0.090	20.9	0		5	3	2
Daubentonia madagascariensis[37]	2800	46.06	0.008	Nosy Mangabe	-0.031	11.4	0	35.6	2	3	3.5
Eulemur albifrons[37]	1811	23.10	0.080	Andranobe, Masoala Nat. Park	-0.046	7.4	0		11	3	
Eulemur fulvus[37]	2300	24.78	0.104	Ampijaroa, Mayotte	0.036	10.9	0	48.6	18	3	2.7
Eulemur macaco[37]	1908	22.65	0.047	Lokobe	0.026	13.1	0	5.3	10	3	2.2
Eulemur mongoz[37]	1212	17.46	0.110	Ampijaroa	0.051	16.9	0	2.9	4	3	2.5
Eulemur rubriventer[37]	2067	24.29	0.132	Ranomafana	-0.076	11.7	0	25	5	3	
Eulemur rufus[37]	2154	22.20	0.106	Ranomafana	-0.051	19.0	0		18	3	3.4
Hapalemur griseus[37]	935	13.74	0.200	Ranomafana	-0.144	9.1	1		6	3	
Indri indri[37]	5830	34.81	0.073	Analamazoatra, Mantadia, Betampona	-0.015	8.1	1	22.5	6	3	7
Lepilemur edwardsi[37]	915	7.24	0.431	Ampijoroa	-0.270	24.0	1		3	3	1.6
Microcebus rufus[37]	46	1.65	0.050	Ranomafana	0.006	10.4	0		4	3	1.8
Phaner furcifer[37]	327	6.75	0.116	Kirindy	0.045	10.0	0		4	3	
Propithecus diadema[37]	6500	38.47	0.175	Mantadia, Tsinjoarivo	-0.127	10.0	0		9	2	5.3

Propithecus edwardsi[37]	5656	37.34	0.127	Ranomafana	-0.071	12.5	0		10	2	
Propithecus verreauxi[37]	3250	26.05	0.169	Ampijaroa, Kirindy	-0.008	20.9	1	5.3	12	2	6
Varecia rubra[37]	3300	29.37	0.019	Andranobe, Masoala Nat. Park	0.015	5.3	0		16	3	
Varecia variegata[37]	3600	30.88	0.088	Nosy Mangabe	-0.038	9.5	0	110.2	16	3	2.7

Note: Abbreviations: BoM = female body mass, ECV = female endocranial volume, N ECV = number of female endocranial volumes averaged, CV = coefficient of variation, LV = leaves, Prec = precipitation, NDVI = Normalized Difference Vegetation Index, P2T = number of dry months, *r* = the mean vector length, an estimate of the concentration of precipitation over the year, SD = standard deviation, Temp = temperature. Diff NDVI = the difference between CV in diet and CV in NDVI[†], a measure of the amount of buffering taking place, see main text. Diff Prec = the difference between CV in diet and CV in Prec[†], a measure of the amount of buffering taking place, see main text.

[†]Environmental data and group size data were taken from same study location as dietary data.

[‡]Environmental data taken from same locations as endocranial volumes were originally from.

[§]Group sizes were from the same study population as where dietary data were from.

[$]Isler, pers. comm.

[*]Body mass taken from same specimens as ECV measurements.

[§]ECV measurements of individuals with unknown locations.

[±]Dietary study of 11 months with 1 estimated value.

[¥]Measurements taken from genus averages

Table A4.2. Multivariate phylogenetic least square (PGLS) model fitting. P-values are shown and the direction of the relationship between brackets. Only a selection of the several models that were tested are shown as illustration. Model 3 had the lowest AIC and was therefore the best fit model.

Variable	**Model 1** ***P***	**Model 2** ***P***	**Model 3** ***P***	**Model 4** ***P***
Environmental seasonality	0.09 (+)	0.03 (+)	0.02 (+)	0.03 (+)
Minimal temperature	0.06 (+)	0.03 (+)	0.09 (+)	
Folivory	0.11 (-)	0.05 (-)	0.0001 (-)	0.0002 (-)
ln Home range	0.70 (-)	0.60 (-)		
Terrestriality	0.93 (-)			
ln Body mass	0.98 (+)			
ln Age first reproduction	0.82 (+)			
ln Group size	0.50 (+)	0.33 (+)		
Residual ECV	0.17 (+)	0.03 (+)	<0.0001 (+)	<0.0001 (+)
AIC	-95.36	-118.58	**-195.86**	-194.84

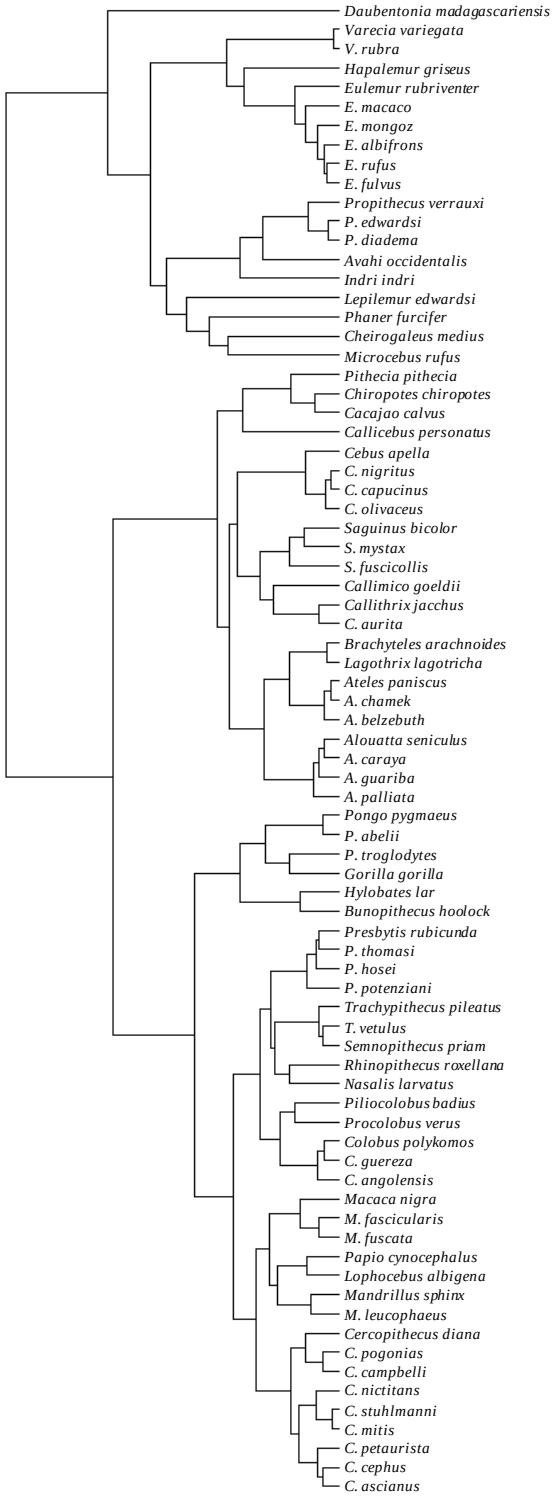

Figure A4.1. Primate phylogeny used in this study.

References appendix Chapter 4

1. Wich, S. A. and Nunn, C. L., Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. Behavioral Ecology and Sociobiology, 2002. 52(6): p. 474-484.
2. Agostini, I., Holzmann, I., and Di Bitetti, M. S., Are howler monkey species ecologically equivalent? Trophic niche overlap in syntopic *Alouatta guariba clamitans* and *Alouatta caraya.* American Journal of Primatology, 2010. 72(2): p. 173-186.
3. Kowalewski, M. M., Patterns of affiliation and co-operation in howler monkeys: an alternative model to explain social organization in non-human primates. 2007, University of Illinois.
4. Chiarello, A. G., Diet of the Brown Howler monkey *Alouatta fusca* in a semi deciduous forest fragment of southeastern Brazil. Primates, 1994. 35(1): p. 25-34.
5. Galetti, M., Pedroni, F., and Morellato, L. P. C., Diet of the Brown Howler monkey *Alouatta fusca* in a forest fragment in Southeastern Brazil. Mammalia, 1994. 58(1): p. 111-118.
6. Stoner, K. E., Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. International Journal of Primatology, 1996. 17(1): p. 1-30.
7. Dunn, J. C., Cristobal-Azkarate, J., and Vea, J. J., Seasonal variations in the diet and feeding effort of two groups of Howlers in different sized forest fragments. International Journal of Primatology, 2010. 31(5): p. 887-903.
8. Julliot, C. and Sabatier, D., Diet of the red howler monkey (*Alouatta seniculus*) in French-Guiana. International Journal of Primatology, 1993. 14(4): p. 527-550.
9. Nunes, A., Foraging and ranging patterns in white-bellied spider monkeys. Folia Primatologica, 1995. 65: p. 85-99.
10. Suarez, S. A., Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. International Journal of Primatology, 2006. 27(2): p. 411-436.
11. Di Fiore, A. and Campbell, C. J., The atelines: Variation in ecology, behavior, and social organization, in Primates in Perspective, C. J. Campbell, Fuentes, A., MacKinnon, K. C., Panger, M., and Bearder, S. K., Editors. 2007, Oxford University Press: New York.
12. Wallace, R. B., Seasonal variation in diet and foraging behavior of *Ateles chamek* in southern Amazonian tropical forest. International Journal of Primatology, 2005. 26(5): p. 1053-1075.
13. Gordon, A. D., Scaling of size and dimorphism in primates II: Macroevolution. International Journal of Primatology, 2006. 27(1): p. 63-105.

14. van Roosmalen, M. G. M., Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. 1980, Landbouwhogeschool Wageningen: Leersum.
15. Strier, K. B., Diet in one group of woolly spider monkeys, or Muriquis (*Brachyteles arachnoides*). American Journal of Primatology, 1991. 23(2): p. 113-126.
16. Talebi, M., Bastos, A., and Lee, P. C., Diet of southern muriquis in continuous Brazilian Atlantic Forest. International Journal of Primatology, 2005. 26(5): p. 1175-1187.
17. Milton, K., Habitat diet and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroy 1806). International Journal of Primatology, 1984. 5(5): p. 491-514.
18. Smith, R. J. and Jungers, W. L., Body mass in comparative primatology. Journal of Human Evolution, 1997. 32(6): p. 523-559.
19. Ayres, J. M. C., Uakaris and Amazonian flooded forest. 1986, University of Cambridge: Cambridge.
20. Müller, K. H., Ahl, C., and Hartmann, G., Geophagy in masked titi monkeys (*Callicebus personatus melanochir*) in Brazil. Primates, 1997. 38(1): p. 69-77.
21. Porter, L. M., Dietary differences among sympatric Callitrichinae in Northern Bolivia: *Callimico goeldii, Saguinus fuscicollis* and *S. labiatus.* International Journal of Primatology, 2001. 22(6): p. 961-992.
22. Martins, M. M. and Setz, E. Z. F., Diet of buffy tufted-eared marmosets (*Callithrix aurita*) in a forest fragment in southeastern Brazil. International Journal of Primatology, 2000. 21(3): p. 467-476.
23. Passamani, M. and Rylands, A. B., Feeding behavior of Geoffroy's marmoset (*Callithrix geoffroyi*) in an Atlantic forest fragment of south-eastern Brazil. Primates, 2000. 41(1): p. 27-38.
24. Araujo, A., Arruda, M. F., Alencar, A. I., Albuquerque, F., Nascimento, M. C., and Yamamoto, M. E., Body weight of wild and captive common marmosets (*Callithrix jacchus*). International Journal of Primatology, 2000. 21(2): p. 317-324.
25. de Castro, C. S. S. and Araújo, A., Diet and feeding behavior of marmoset, *Callithrix jacchus*. Brazilian Journal of Ecology, 2007. 7: p. 14-19.
26. Zhang, S. Y., Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French-Guiana. International Journal of Primatology, 1995. 16(3): p. 489-507.
27. Perry, S. and Ordoñez Jiménez, J. C., The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics, in Feeding Ecology in Apes and Other Primates, G. Hohmann, Robbins, M. M., and Boesch, C., Editors. 2007, Cambridge University Press. p. 203-234.

28. Galetti, M. and Pedroni, F., Seasonal diet of Capuchin monkeys (*Cebus apella*) in a semideciduous forest in South-East Brazil. Journal of Tropical Ecology, 1994. 10: p. 27-39.
29. Robinson, J. G., Seasonal variation in use of time and space by the wegde-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory, in Smithsonian contributions to zoology. 1986: Washington.
30. Peetz, A., Ecology and social organization of the Beared Saki *Chiropotes satanas chiropotes* (Primates: Pitheciinae) in Venezuela. Ecotropical Monographs, 2001. 1: p. 1-170.
31. Di Fiore, A. and Rodman, P. S., Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a neotropical terra firma forest. International Journal of Primatology, 2001. 22(3): p. 449-480.
32. Norconk, M. A., Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela, in Adaptive radiations of neotropical primates, M. A. Norconk, Rosenberger, A. L., and Garber, P. A., Editors. 1996, Plenum Press: New York. p. 403-423.
33. Egler, S. G., Feeding ecology of *Saguinus bicolor bicolor* (Callitrichidae, Primates) in a relict forest in Manaus, Brazilian Amazonia. Folia Primatologica, 1992. 59(2): p. 61-76.
34. Ford, S. M. and Davis, L. C., Systematics and body size: Implications for feeding adaptations in New World monkeys. American Journal of Physical Anthropology, 1992. 88(4): p. 415-468.
35. Peres, C. A., Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins in an Amazonian Terra Firme Forest. Journal of Zoology, 1993. 230: p. 567-592.
36. van Woerden, J. T., van Schaik, C. P., and Isler, K., Large brains buffer energetic effects of seasonal habitats in catarrhine primates. Evolution, 2011. doi:10.1111/j.1558-5646.2011.01434.x.
37. van Woerden, J. T., van Schaik, C. P., and Isler, K., Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. American Naturalist, 2010. 176(6): p. 758-767.

Chapter 5.

General Discussion

The aim of this thesis was to contribute to solving a major question in brain size evolution: why did the brains of some primates grow so large? I integrated an energetic-cost perspective and a benefit perspective of ecological factors, by investigating the influence of seasonal periods of food shortage on brain size evolution in primates. In this thesis I tested two complementary hypotheses. First, the Expensive Brain hypothesis (Isler and van Schaik 2009a), from the cost-perspective, predicts a constraint of experienced seasonality on brain size evolution. Second, the Cognitive Buffer hypothesis (Allmann et al. 1993; Deaner et al. 2003; Sol 2009) focuses on the benefits of larger brains in seasonal habitats, predicting a positive relationship between the two.

One of the most important outcomes of this study is that the two hypotheses can be reconciled. They can best be seen as two processes which operate at the same time. The key to acknowledge this is to consider costs imposed by seasonal troughs in energy intake (by assessing how much energy intake fluctuates over the year, and thus the seasonality experienced by the animal) separately from the cognitive buffer effects (by looking at whether the energy intake fluctuates less than would be expected from fluctuations in food availability). Measured as such, we could show that larger-brained primates in general experience less fluctuation in their energy intake than smaller brained primates, at least in part because they manage to buffer environmental fluctuations through cognitive solutions. However, the degree to which they cognitively buffer their environmental seasonality differs, with the lemurs showing a weaker trend than the Old and New World primates. We found that a certain degree of habitat seasonality needs to be present for cognitive buffering, but we also found that largely folivorous primates show less cognitive buffering than frugi/omnivorous primates, even after controlling for their overall smaller brain size. In conclusion, we have shown that an energetic perspective of ecological conditions can explain a considerable amount of variation in brain size evolution in primates.

Limitations of the current approach

In this study, we found clear evidence for both the expensive brain effect and for the presence of cognitive buffering. Our measures for net energy intake and buffering were necessarily quite crude, but the positive findings suggest the effects were strong because it is unlikely that these effects are found spuriously. Nonetheless, it is instructive what new insights could be gained from improving the quality of the various estimates.

The measure we used to assess experienced seasonality, coefficient of variation (CV) in diet, has several limitations. First, measuring only dietary intake fails to take into account seasonal differences in energy expenditure. Variation in field metabolic rate would be a much more precise measure of experienced seasonality. However, this kind of data is very rarely studied in wild populations (e.g. Nagy and Milton 1979; Schmid and Speakman 2000; Tsuji et al. 2008). The doubly-labeled water technique depends on a precisely measured intake of the prescription fluid, and has therefore been limited to semi-free primate groups (e.g. Pontzer et al. 2010). The presence of urinary ketone indicates a negative energy balance (Knott 1998), but perhaps only in severe conditions (Leendertz et al. 2010). Newly developed hormonal techniques such as urinary C-peptides (e.g. Deschner et al. 2008) can indicate a positive or negative energy balance in wild primates (e.g. Emery Thompson and Knott 2008; Emergy Thompson et al. 2009), which eventually will open up new avenues for comparative studies. At present, to obtain a reasonable sample size for interspecific comparisons, measuring dietary intake from observational studies remains the best option. Including an estimate of energy expenditure from seasonal ranging patterns or activity budgets would, however, be feasible.

Second, our measure of food quality is rather crude. It is composed of feeding time times the relative energy content. Virtually all studies report feeding time rather than actual amount ingested, and we were forced to assume that mean intake rates per unit time are the same for each food item. This limitation can in principle be alleviated by field estimates of food intake rates for each food item, but understandably very few studies have managed this (e.g. Knott 1998), and the errors involved are not known, but are expected to be large. We also used average relative caloric contents for broad food categories (8 for insects, 5 for fruit/flower/seeds, 3 for young leaves, 1 for mature leaves as calculated from gram crude fiber per kg dry matter by Langer 2003). This simple measure was chosen here because most reports of feeding behavior by convention utilize broad classifications of food types. Although some studies report the consumption rates of

individual plant species, they do not distinguish between different parts of that plant (e.g. buds, young or mature leaves, stems, fruit pulp etc.), which may differ considerably in nutritional content (which is largely unknown). Therefore, only a crude classification allowed us to include a large number of species in our comparisons. However, instead of looking at diet quality as a proxy of caloric content, one could also investigate digestibility (protein per condensed tannin and fiber, e.g. Beeson 1989) which would estimate how much energy can actually be extracted from the food source. With a reasonable sample of species, it would be interesting to consider more details, such as whether protein or carbohydrate availability is more limiting, or whether morphological specializations such as the size of the liver correlate with the digestibility of fallback foods.

Finally, in combination with the unavoidable crudity of our measure and potential error variation due to combining various behavioral data from different researchers, our limited sample size may explain why we only found a weak cognitive buffering effect in the lemurs. It remains unclear whether this reflects a special case of Madagascar or whether this is an effect of methodological inaccuracy. The limited sample size in the New World monkeys may also explain why the results in this group were less stable than in catarrhines.

Suggestions for future research

Two important factors were not taken into account in this thesis due to practical limitations: First, physiological buffers and second, unpredictability, i.e. variation *between* years.

As mentioned in the introduction, there are two types of buffers, cognitive and physiological buffers, to deal with seasonality of food availability, of which the latter ones were not considered in this thesis. There are several possible physiological adaptations that buffer seasonality; one is by storing fat during the periods of food abundance. Small lemurs of the family Cheirogaleidae are known for storing fat in their tails. Mouse and (fat-tailed) dwarf lemurs (*Microcebus spp.* and *Cheirogaleus spp.* resp.) can increase their body mass and tail circumference between 30 to 90% before going into hibernation or torpor (Fietz 1998; Schmid 1999; Dausmann et al. 2004, 2005). Other primates may store major fat reserves to gain a positive energy balance which they need to enter the reproductive cycle (Knott 1998; Knott 2005). Navarette et al. (in rev.) found a negative relationship between fat storage and relative brain size in a broad sample of mammals (N=100 species). They proposed that encephalization

and fat storage are compensatory strategies to buffer against starvation, because costs of transport increase with total body mass, and fat storage is therefore energetically costly, although adipose tissue is metabolically not expensive. However, in their primate sample (N= 22 species), this trade-off was not found. They argue that this may be due to a methodological problem, as their estimated fat storage was based on abdominal fat, which is not necessarily the location for fat storage in primates (e.g. fat-tailed dwarf lemur, *C. medius*). A direct comparison of adipose depots with seasonality measures from my study was not feasible as the overlap in species between the two studies was very small. As obtaining intact primate cadavers is difficult, and measuring adipose depots from living animals depends on calibration with sacrificed individuals, it would be desirable to derive a measure of fat storage from readily available non-invasive measurements. If an animal stores fat during parts of the year, the variation in body *mass* will be larger than expected from variation in body *size* (cf. Altmann et al. 1993). In a preliminary study, I therefore calculated a "fat index" as the residual body mass variation, by using endocranial volume as a proxy of body size. I did not find a significant relationship between this fat index and neither cognitive buffering nor experienced seasonality or relative brain size (data now shown). However, the relationships were in the predicted direction (negative with cognitive buffering and relative brain size). Therefore, it might be worthwhile to pursue this direction of research in the future.

Second, our data on experienced seasonality mostly reflect variation in food intake within a year. Primates are relatively long-lived and therefore face the challenges of between-year variation, that is, unpredictability in addition to the regular within year variation. Relatively infrequent, but completely unpredictable periods of extreme conditions may put severe constraints on brain size in those animals with a slow life-history pace (and thus low fertility and population growth rates), which cannot buffer catastrophic events through fluctuations in population size. For primates, examples of unpredictable habitats are areas affected by El-Niño droughts in South-East Asia, which are highly unpredictable between years (Dewar and Wallis 1999; Wich and van Schaik 2000; Dewar 2003). Another is eastern Madagascar. Even though the seasonal fluctuation of plant productivity is fairly moderate compared to the western, more dry part of Madagascar, catastrophic cyclones and storms make it very unpredictable (Richard and Dewar 1991; Wright 1999). Physiological buffers, such as seasonal breeding or hibernation, are expected only to buffer against predictable seasonality, i.e. when the lean period always falls within the same time of the year. However, in habitats where the periods of food scarcity are

unpredictable, physiological buffers do not help. Thus, the constraints may be so strong that, as in extremely seasonal climates, cognitive buffering is not able to overcome the starvation. If so, taking unpredictability into account may resolve the question whether lemurs are actually unable to cognitively buffer their environment, or whether this is merely a result of measurement inaccuracies. Considering unpredictability in addition to seasonality may also be important when investigating other mammalian orders.

Despite these limitations, the surprisingly clear findings of this thesis open up many questions in related fields. In birds, evidence of cognitive buffering comes from several studies. For example, migrating bird species have smaller brains than non-migrating species (Winkler et al. 2004; Sol et al. 2005), which can be reflecting a cognitive buffer effect in the residential species (Sol et al. 2005) or a reduced selective advantage of enhanced cognitive performance in migratory species (Sol et al. 2010). It could, however, also represent higher energetic costs of migration itself (Piersma 1998, 2002) and therefore a trade-off between the costs of long distance flight and the brain. Schuck-Paim et al. (2008) found a direct positive relationship between climatic variability and relative brain size in Neotropical parrots, but the results differ depending on seasonal migration patterns: In species that moved from a forest to an open habitat, brain size correlates with seasonal variation in temperature, whereas brain size correlates with seasonal variation in precipitation in those species that did not move between habitats. It would be interesting to test whether cognitive buffering as defined in this thesis – the variation in the difference between environmental and experienced seasonality – also applies in birds and whether experienced energetic constraints of seasonality are important in this group as well.

We expect the effects of energetic constraints to prevail if animals cannot move into other habitats or if a dietary switch to explore hidden high-quality food sources is somehow prevented (through e.g. specialized digestive tract which cannot make use of energy-rich food items, Clauss et al. 2008). A high energy consumption of the brain relative to total metabolism and high extrinsic (unavoidable) mortality further reduce the feasibility of cognitive buffering. Thus, we expect cognitive buffer effects to be most apparent in the following categories of animals: (i) animals that can fly or swim and thus easily sample other habitats or move into other regions, such as birds, bats and some classes of marine mammals, (ii) animals that can more easily cope with minor reductions in food availability because their brains usurp only a relatively modest portion of the energy budget, in particular due to large body size, such as large carnivores; and (iii) animals that rely on extractive foraging, food caching, or that exploit dispersed food patches.

In lineages lacking these features, especially smaller nonvolant mammals, the energetic constraint effects are more likely to predominate, leading to a negative correlation between brain size and both environmental and experienced seasonality.

Exceptions to Marsh's Rule

From a macroevolutionary perspective, the results of this thesis may help to understand why Marsh's Rule does not lead to ever-increasing encephalization in all lineages, i.e. why there are lineages in which brain size remains stable or even decreases in over time, even in mammals (Safi et al. 2005; Montgomery et al. 2010). We expect brain size to be constrained in any situation in which there are periods of unavoidable starvation. Indeed, orangutans suffering from periods of unavoidable starvation due to the El Niño droughts have been shown to exhibit relatively small brains (Taylor and van Schaik 2007). And in birds, cuckoos living in poorer habitats are reported to have smaller brains than those living in richer habitats (Boerner and Krüger 2008). More general, mammals living on small islands have been suggested to evolve smaller brains in order to cope with resource shortages (Filin and Ziv 2004; Köhler and Moyà-Solà 2004; Lomolino 2005; Niven 2005; Weston and Lister 2009).

Of immediate interest for evolutionary anthropologists is the case of the tiny-bodied and even tinier-brained hominin from the island of Flores, called the "hobbit" (Falk et al. 2005). The dwarfing pattern seen in *Homo floresiensis* fits this trend of ecological adaptation to extreme food shortage, as other island mammals such as Malagasy dwarf hippopotamus also had very small brains (Weston and Lister 2009). Does island dwarfing impact brain size even more than body size, through the strong constraints of unavoidable periodic food shortages? As Montgomery et al. (2010) analyses revealed, brain size reductions occurred within the primate lineage. Thus, the only unexpected aspect of *H. floresiensis*' evolution is the rate at which brain size probably decreased. Of course this interpretation depends on the assumed starting point, which may have been an early *Homo* (Baab and McNulty) with an even smaller brain size than the Dmanisi *Homo erectus* with 650cc (Gabundia et al. 2000). Some evidence exists that morphological evolution is accelerated on islands (Millien 2006, 2011), although others did not find evidence for such acceleration (Meiri et al. 2011; Raia and Meiri 2011). Future research should clarify whether the hobbit's small brain size can be the result of secondary reduction, rather than be indicative of a more ancestral state.

From our results it has become clear that ecological challenges can explain a considerable portion of brain size variation (up to 40%), when they are assessed from the animals' perspective. The next step would be to integrate this approach with the other major factor playing a role in brain size variation, the tradeoff between investment in brain size or in growth and reproduction, which have been proposed to explain the correlations between brain size and life history traits and developmental patterns (Isler and van Schaik 2006a; Isler and van Schaik 2006b; Isler et al. 2008; Isler and van Schaik 2009a, b; Isler 2011). Correlations between life history pace and brain size have been known to exist for a long time (Sacher 1959; Harvey and Bennett 1983), but the direction of causality is debated. On one hand, cognitive abilities may increase survival, and thus ultimately lifespan and the larger brain size this requires will, in turn, enforce longer development periods, at least in precocial birds and mammals. But on the other hand, only a prolonged development period may allow for enough time to learn complex skills (Deaner et al. 2003).

At present, it seems that the skill learning hypothesis is not supported by empirical data, as altricial mammals do not show a correlation between the duration of development periods and relative brain size (Isler and van Schaik 2009a), and immature orangutans attain all necessary skills years before they reach reproductive maturity (Jaeggi et al. 2010). Therefore, the causal arrow seems to go from brain size to life history pace. In other words, there may be many species with a slow life history, but not necessarily large brains (such as albatrosses, or Sirenia), but no species with large brains and a relatively fast development time. However, as the constraint is energetic in nature and independent of time, species which are able to invest a large amount of energy in their offspring (e.g. by getting help from other group members) are exempted from the latter rule and may show a combination of fast development and relatively large brains (e.g. canid carnivores, Isler and van Schaik 2009a). In general, though, the trade-off between production and brain size places a limit on ever-increasing encephalization, as the population growth rates will eventually get too low to allow recovery from catastrophic population crashes (the "gray ceiling" to brain size for a lineage, Isler and van Schaik 2009b). It would be interesting to see whether extreme habitat seasonality, or unpredictable periods of unavoidable starvation, can predict the value of this threshold in addition to general predictors such as predation risk or development type.

In conclusion, both the trade-off between production and brain size, and the constraint through seasonality are counterbalancing Marsh's rule on a macroevolutionary scale, and can explain why the overall trend to increase brain size does not invariably hold in all lineages. What

we have learned here might help us in the future to integrate all the costs of brain size evolution.

Integrating the costs and the benefits of encephalization

Hypotheses that try to explain brain size evolution through the benefits of cognitive abilities can be put in broad categories: those explaining variation in brain size as a way of dealing with "social complexity", those focusing on "ecological complexity" and those considering "general behavioral flexibility" (Figure 5.1).

First, hypotheses on "social complexity" are summarized under the so-called *social brain hypothesis* (Byrne and Whiten 1988; Sawaguchi 1992; Dunbar 1998). This hypothesis was originally developed to explain the special intelligence attributed to monkeys and apes (Humphrey 1976) as adaptations for dealing with the distinctive complexities of their social lives (Byrne and Whiten 1988; Dunbar 1998). This hypothesis has found broad acceptance (Dunbar 2009), although empirical tests of this hypothesis yielded somewhat inconsistent results. Some studies used social group size as a proxy for social complexity and found a positive correlation with neocortex ratio – a proxy of intelligence – in primates (Dunbar 1992) and carnivores, but not in insectivores or ungulates (Dunbar 1998; Shultz and Dunbar 2006). Even within primates, the positive correlation only holds for haplorhine primates (MacLean et al. 2009). As group size was found not to correlate with relative brain size in nonprimate mammals (Shultz and Dunbar 2007), pair-bondedness was now taken as exerting cognitive demands in these taxa. Some studies on the social brain hypotheses have taken ecological factors into account in their analyses (e.g. Dunbar and Shultz 2007), incorporating crude measures such as dietary types as potentially confounding factors.

Second, other hypotheses have focused on the necessity to deal with ecological complexity, such as the *technical intelligence hypothesis* (Byrne 1997) and its relative, the *extractive foraging hypothesis* (Parker and Gibson 1979; Gibson 1990). These hypotheses relate the required larger brains and greater intelligence to extract embedded, hidden food sources (such as nut cracking or digging for insects), which often require complex object manipulation. In support of this hypothesis, all great apes and the relatively large brained capuchin monkeys show food extraction of processing techniques that are technically demanding in some way, whereas other monkeys do not. However, Dunbar (1995) did not find a difference in neocortex ratio between extractive and non-extractive foragers. The *cognitive buffering hypothesis* (Allmann et

al. 1993; Deaner et al. 2003; Sol 2009) also focuses on dealing with ecologically complex habitat conditions, such as seasonal or novel environments. This hypothesis is extensively discussed throughout this thesis, and we found support for it also in primates.

Finally, some researchers focus on *general behavioral flexibility,* incorporating social and ecological complexity and stating that larger brains generate increased general intelligence necessary to deal with either social or ecological complexity, or a combination of both (e.g. Reader and Laland 2002; Reader et al. 2011). This approach suggests that ecologically relevant cognitive abilities (extractive foraging, dietary breadth, frugivory) and elements of cultural intelligence (social learning) are important parts of general intelligence, and are the most likely candidates for a positive selection pressure on encephalization (Reader et al. 2011). Their research, however, suggests that rather than domain-specific, general intelligence is, as the name implies, domain-general (Johnson et al. 2002; Deaner et al. 2007), rendering it almost impossible to extricate the initial factor responsible for fitness benefits of larger brains. Identifying the ultimate positive selection pressure that explains brain size variation is probably impossible, because once the cognitive skills are advanced, they are applied in all contexts (Reader et al. 2011).

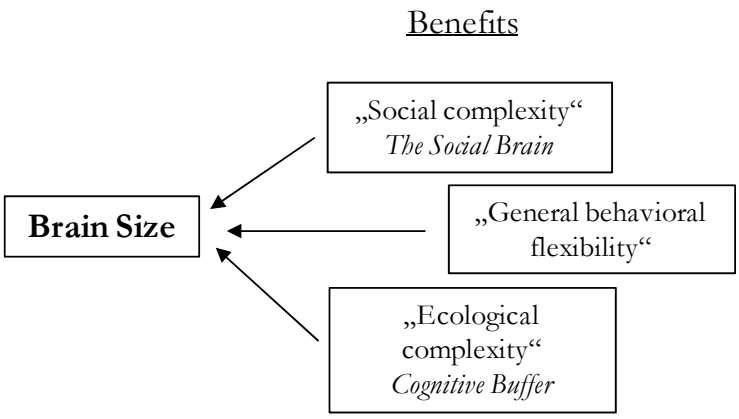

Figure 5.1. Three broad categories of hypotheses on the selective pressures (benefits) that acted on brain size to increase encephalization.

These theories on the benefits perspective argue that to be able to grow larger brain, a species must overcome the constraints through a strong selective pressure, in other words larger brains must have a considerable fitness benefit. Exponents of this approach assume that the benefits must be strong enough to overcome the costs, and therefore largely ignore the latter. In contrast with this view, we argue that overcoming the costs is the crucial point, because the ability to do so varies according to many species-specific characteristics, whereas benefits of enhanced cognition may be rather ubiquitous. The *expensive brain framework* (Isler and van Schaik 2009a) thus explicitly focuses on the costs of brain size, stating that the evolution of a relatively larger brain is only possible if overall energy throughput is increased, energy is distributed differently, or a combination of both. However, once the costs are met, a differential expression of benefits according to socio-ecological conditions may explain additional variation in relative brain size. This combined approach is the one taken in this thesis.

The cost and benefit perspectives on brain size evolution can be combined into one big diagram (Figure 5.2). The right side of the figure represents the benefits of enhance cognitive abilities, and the left side the energetic constraints on brain size. If these costs are met by increasing or stabilizing energy throughput, relatively larger brains can evolve, and will do so because the benefits are ubiquitous (note the change in direction of the arrows between brains and the benefits in comparison with Figure 5.1).

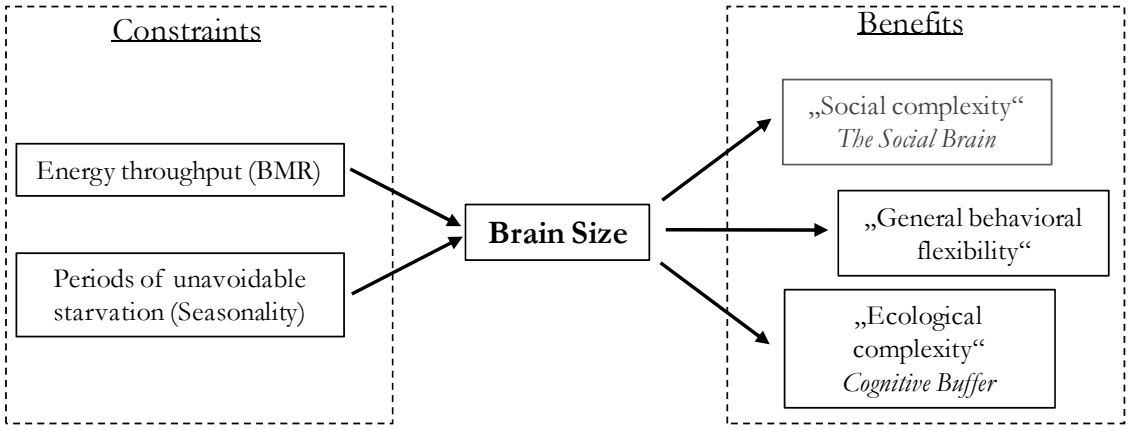

Figure 5.2. Costs and benefits incorporated into one graphical representation. See text for explanation.

From this template, it becomes clear that both costs and benefits should be incorporated in a single model to see whether additional variation in brain size is explained by benefits, or whether benefits are explaining so much of brain size variation that incorporating costs is not essential. Results of this thesis (appendices of Chapters 2, 3 and 4) show that, once the energetic constraint of seasonality is accounted for, group size as a crude proxy of social complexity is no longer significantly correlated with brain size in all major groups of primates (Table 5.1a). Also, large-brained primates apply cognitive buffering without any interference of group size or social complexity (see chapter 4). Therefore, our preliminary conclusion is that there is no additional predictive power of social complexity on relative brain size, once the energetic costs are considered. Additional support is provided by the fact that there are primate species which are mostly solitary, but nevertheless relatively and absolutely large-brained (orangutans and aye-ayes). The existence of such species cannot be explained from the social brain hypothesis, as no alternative selective pressures to evolve a large brain apart from living in complex social groups are allowed. In sum, the results presented throughout this thesis do not support the prediction of the social brain hypothesis.

Table 5.1. Phylogenetic least square (PGLS) analyses with brain size as response variable, body mass as covariate and costs (experienced seasonality) and benefits (group size and cognitive buffering) as possible explanatory variables.

	Variable (N=75)	**lambda**	**Estimate**	**Std. Error**	**t-value**	**p**
a	Experienced seasonality	0.984	-1.30	0.30	-4.29	<0.0001
	Group size		0.02	0.04	0.51	0.61

	Variable (N=75)	**lambda**	**Estimate**	**Std. Error**	**t-value**	**p**
b	Experienced seasonality	0.995	-0.70	0.34	-2.01	0.04
	Cognitive buffering		0.54	0.24	2.31	0.02

	Variable (N=75)	**lambda**	**Estimate**	**Std. Error**	**t-value**	**p**
c	Experienced seasonality	0.995	-0.74	0.38	-1.93	0.05
	Cognitive buffering		0.54	0.25	2.12	0.04
	Group size		0.01	0.03	0.23	0.82

But if we build a model including both the "ecological complexity" aspect of encephalization benefits, represented by our measure of cognitive buffering, together with the energetic costs of seasonality, represented by our measure of experienced seasonality, both effects remain significant (Table 5.1b), also when group size is included (Tabel 5.1c). This means that, in addition to costs, different ways to deal with ecological complexity do indeed explain a significant part of brain size variation in primates. Eventually, integration with the life-history tradeoffs may provide an even more comprehensive picture of brain size evolution.

In conclusion, these results indicate that in order for social benefits to arise, successful solutions to ecological problems are required first. At present, there is no evidence for an independent role of social benefits, once the costs have been accounted for. Our integrative approach offers the hitherto most comprehensive explanation for the variation in brain size in all primates. All together, the results of this thesis show that ecological conditions play a major role in explaining brain size variation among primates.

Bibliography

Aiello, L. C., and P. Wheeler. 1995. The expensive tissue hypothesis - the brain and the digestive system in human and primate evolution. Current Anthropology 36:199-221.

Akaike, H. 1974. New look at statistical model identification. Ieee Transactions on Automatic Control Ac19:716-723.

Albrecht, G. H., P. D. Jenkins, and L. R. Godfrey. 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. American Journal of Primatology 22:1-50.

Allmann, J., T. McLaughlin, and A. Hakeem. 1993. Brain weight and life span in primate species. Proceedings of the National Academy of Sciences of the United States of America 90:118-122.

Altmann, J., D. Schoeller, S. A. Altmann, P. Muruthi, and R. M. Sapolsky. 1993. Body size and fatness of free-living baboons reflect food availability and activity levels. American Journal of Primatology 30:149-161.

Altmann, S. 1998. Foraging for survival: yearling Baboons in Africa. University of Chicago Press.

Armstrong, E. 1983. Relative brain size and metabolism in mammals. Science 220:1302-1304.

Arnold, C., L. J. Matthews, and C. L. Nunn. 2010. The 10k Trees Website: a new online resource for primate phylogeny. Evolutionary Anthropology 19:114-118.

Baab, K. L., and K. P. McNulty. 2009. Size, shape, and asymmetry in fossil hominins: the status of the LB1 cranium based on 3D morphometric analyses. Journal of Human Evolution 57:608-622.

Barrickman, N. L., and M. J. Lin. 2010. Encephalization, expensive tissues, and energetics: An examination of the relative costs of brain size in strepsirrhines. American Journal of Physical Anthropology 143:579–590.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London.

Beattie, J. C., A. T. C. Feistner, N. M. O. Adams, P. Barker, and J. B. Carroll. 1992. First captive breeding of the aye-aye, *Daubentonia madagascariensis*. Dodo 28:23-30.

Beeson, M. 1989. Seasonal dietary stress in a forest monkey (*Cercopithecus mitis*). Oecologia 78:565-570.

Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. Nature 446:507-512.

Boerner, M., and O. Krüger. 2008. Why do parasitic cuckoos have small brains ? Insights from evolutionary sequence analyses. Evolution 62:3157-3169.

Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. Global Change Biology 12:862-882.

Byrne, R. W. 1997. The Technical Intelligence hypothesis: an additional evolutionary stimulus to intelligence? . Pp. 289-311 *in* A. Whiten, and R. W. Byrne, eds. Machiavellian Intelligence II: Extensions and Evaluations. Cambrigde University Press.

Byrne, R. W., and A. Whiten. 1988. Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. University Press, Oxford.

Catlett, K. K., G. T. Schwartz, L. R. Godfrey, and W. L. Jungers. 2010. "Life History Space": A multivariate analysis of life history variation in extant and extinct Malagasy lemurs. American Journal of Physical Anthropology 143:391-404.

Charles-Dominique, P. 1974. Ecology and feeding behavior of five sympatric lorisids in Gabon. Pp. 131-150 *in* R. D. Martin, G. A. Doyle, and A. C. Walker, eds. Prosimian Biology. Duckworth Press, London.

Clauss, M., W. J. Streich, C. L. Nunn, S. Ortmann, G. Hohmann, A. Schwarm, and J. Hummel. 2008. The influence of natural diet composition, food intake level, and body size on ingesta passage in primates. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 150:274-281.

Clutton-Brock, T. H., and P. H. Harvey. 1980. Primates, Brains and Ecology. Journal of Zoology 190:309-323.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103-137.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305-335.

Dausmann, K. H., J. Glos, J. U. Ganzhorn, and G. Heldmaier. 2004. Physiology: Hibernation in a tropical primate. Even in the wound-down hibernating state, this lemur can warm up without waking up. Nature 429:825-826.

Dausmann, K. H., J. Glos, J. U. Ganzhorn, and G. Heldmaier. 2005. Hibernation in the tropics: lessons from a primate. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 175:147-155.

Deaner, R. O., R. A. Barton, and C. P. van Schaik. 2003. Primate brains and life histories: renewing the connection. Pp. 233–265 *in* P. M. Kappeler, and M. E. Pereira, eds. Primate life histories and socioecology. The University of Chicago Press, Chicago, IL.

Deaner, R. O., K. Isler, J. Burkart, and C. van Schaik. 2007. Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. Brain Behavior and Evolution 70:115-124.

Dechmann, D. K. N., and K. Safi. 2009. Comparative studies of brain evolution: a critical insight from the Chiroptera. Biological Reviews 84:161-172.

Deschner, T., J. Kratzsch, and G. Hohmann. 2008. Urinary C-peptide as a method for monitoring body mass changes in captive bonobos (Pan paniscus). Hormones and Behavior 54:620-626.

Dewar, R. E. 2003. Rainfall variability and subsistence systems in Southeast Asia and the Western Pacific. Current Anthropology 44:369-388.

Dewar, R. E., and A. F. Richard. 2007. Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences of the United States of America 104:13723-13727.

Dewar, R. E., and J. R. Wallis. 1999. Geographical patterning of interannual rainfall variability in the tropics and near tropics: An L-moments approach. Journal of Climate 12:3457-3466.

Drake, J. M. 2007. Parental investment and fecundity, but not brain size, are associated with establishment success in introduced fishes. Functional Ecology 21:963-968.

Dunbar, R. I. M. 1992. Neocortex size as a constraint on group size in primates. Journal of Human Evolution 22:469-493.

Dunbar, R. I. M. 1995. Neocortex size and group size in primates: a test of the hypothesis. Journal of Human Evolution 28:287-296.

Dunbar, R. I. M. 1998. The social brain hypothesis. Evolutionary Anthropology 6:178-190.

Dunbar, R. I. M. 2009. The social brain hypothesis and its implications for social evolution. Annals of Human Biology 36:562-572.

Dunbar, R. I. M., and S. Shultz. 2007. Understanding primate brain evolution. Philosophical Transactions of the Royal Society B-Biological Sciences 362:649-658.

Economos, A. C. 1980. Brain-life span conjecture: a re-evaluation of the evidence. Gerontology 26:82-89.

Eeley, H. A. C., and R. A. Foley. 1999. Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodiversity and Conservation 8:1033-1056.

Emery Thompson, M., and C. D. Knott. 2008. Urinary C-peptide of insulin as a non-invasive marker of energy balance in wild orangutans. Hormones and Behavior 53:526-535.

Emery Thompson, M., M. N. Muller, R. W. Wrangham, J. S. Lwanga, and K. B. Potts. 2009. Urinary C-peptide tracks seasonal and individual variation in energy balance in wild chimpanzees. Hormones and Behavior 55:299-305.

Falk, D., C. Hildebolt, K. Smith, M. J. Morwood, T. Sutikna, P. Brown, Jatmiko, E. W. Saptomo, B. Brunsden, and F. Prior. 2005. The brain of LB1, Homo floresiensis. Science 308:242-245.

Fichtel, C., and P. M. Kappeler. 2010. Human universals and primate symplesiomorphies: establishing the lemur baseline. Pp. 395-427 *in* J. B. Silk, and P. M. Kappeler, eds. Mind the Gap. Tracing the origins of human universals. Springer, Berlin Heidelberg.

Fietz, J. 1998. Body mass in wild *Microcebus murinus* over the dry season. Folia Primatologica 69:183-190.

Filin, I., and Y. Ziv. 2004. New theory of insular evolution: unifying the loss of dispersability and body-mass change. Evolutionary Ecology Research 6:115-124.

Fish, J. L., and C. A. Lockwood. 2003. Dietary constraints on encephalization in primates. American Journal of Physical Anthropology 120:171-181.

Gabunia, L., A. Vekua, D. Lordkipanidze, C. C. Swisher, R. Ferring, A. Justus, M. Nioradze, M. Tvalchrelidze, S. C. Anton, G. Bosinski, O. Joris, M. A. de Lumley, G. Majsuradze, and A. Mouskhelishvili. 2000. Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting, and age. Science 288:1019-1025.

Ganzhorn, J. U. 1995. Cyclones over Madagascar - Fate or Fortune. Ambio 24:124-125.

Ganzhorn, J. U., J. Fietz, E. Rakotovao, D. Schwab, and D. Zinner. 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar. Conservation Biology 13:794-804.

Genoud, M. 2002. Comparative studies of basal rate of metabolism in primates. Evolutionary Anthropology 11 (suppl. 1):108-111.

Gibson, K. R. 1986. Cognition, brain size and the extraction of embedded food resources. Pp. 93-103 *in* J. G. Else, and P. C. Lee, eds. Primate Ontogeny, Cognition and Social Behaviour. Cambridge University Press, New York.

Gibson, K. R. 1990. New perspectives on insights and intelligence: brain size and teh emergence of hierarchical mental constructional skills *in* S. T. Parker, and K. R. Gibson, eds. "Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives. Cambridge University Press, Cambridge.

Godfrey, L. R., K. E. Samonds, W. L. Jungers, and M. R. Sutherland. 2001. Teeth, brains, and primate life histories. American Journal of Physical Anthropology 114:192-214.

Godfrey, L. R., G. M. Semprebon, W. L. Jungers, M. R. Sutherland, E. L. Simons, and N. Solounias. 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. Journal of Human Evolution 47:145-169.

Groves, C. P. 2000. The genus *Cheirogaleus*: Unrecognized biodiversity in dwarf lemurs. International Journal of Primatology 21:943-962.

Harcourt, C. 1986. Seasonal variation in the diet of South African Galagos. International Journal of Primatology 7:491-506.

Harris, T. R., C. A. Chapman, and S. L. Monfort. 2010. Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. Behavioral Ecology 21:46-56.

Harvey, P. H., and P. M. Bennett. 1983. Brain size, energetics, ecology and life history patterns. Nature 306:314-315.

Harvey, P. H., and M. D. Pagel. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Healy, S. D., and C. Rowe. 2007. A critique of comparative studies of brain size. Proceedings of the Royal Society B-Biological Sciences 274:453-464.

Hemingway, C. A., and N. Bynum. 2005. The Influence of Seasonality on Primate Diet and Ranging. Pp. 57-104 *in* D. A. Brockman, and C. P. van Schaik, eds. Seasonality in Primates. Cambridge University Press, New York.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

Hofman, M. A. 1983. Energy metabolism, brain size and logevity in mammals. The Quarterly Review of Biology 58:495-512.

Holliday, M. A. 1971. Metabolic rate and organ size during growth from infancy to maturity and during late gestation and early infancy. Pediatrics 47:169-179.

Horvath, J. E., D. W. Weisrock, S. L. Embry, I. Fiorentino, J. P. Balhoff, P. Kappeler, G. A. Wray, H. F. Willard, and A. D. Yoder. 2008. Development and application of a phylogenomic toolkit: Resolving the evolutionary history of Madagascar's lemurs. Genome Res 18:489-499.

Humphrey, N. K. 1976. The social function of intellect. Pp. 303-317 *in* P. P. G. Bateson, and R. A. Hinde, eds. Growing Points in Ethology. Cambridge University Press, Cambridge.

Isler, K. 2011. Energetic trade-offs between brain size and offspring production: Marsupials confirm a general mammalian pattern. Bioessays 33:173-179.

Isler, K., E. C. Kirk, J. M. A. Miller, G. A. Albrecht, B. R. Gelvin, and R. D. Martin. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. Journal of Human Evolution 55:967-978.

Isler, K., and C. van Schaik. 2006a. Costs of encephalization: the energy trade-off hypothesis tested on birds. Journal of Human Evolution 51:228-243.

Isler, K., and C. P. van Schaik. 2006b. Metabolic costs of brain size evolution. Biology Letters 2:557-560.

Isler, K., and C. P. van Schaik. 2009a. The Expensive Brain: A framework for explaining evolutionary changes in brain size. Journal of Human Evolution 57:392-400.

Isler, K., and C. P. van Schaik. 2009b. Why are there so few smart mammals (but so many smart birds)? Biology Letters 5:125-129.

Jaeggi, A. V., L. P. Dunkel, M. A. Van Noordwijk, S. A. Wich, A. A. L. Sura, and C. P. Van Schaik. 2010. Social learning of diet and foraging skills by wild immature bornean orangutans: implications for culture. American Journal of Primatology 72:62-71.

Janson, C. H., and C. A. Chapman. 1999. Resources and primate community structure. Pp. 237–267 *in* J. G. Fleagle, C. H. Janson, and K. E. Reed, eds. Primate communities. Cambridge University Press, Cambridge.

Janson, C. H., and J. Verdolin. 2005. Seasonality of Primate Births in Relation to Climate. Pp. 307-350 *in* D. A. Brockman, and C. P. van Schaik, eds. Seasonality in Primates. Cambridge University Press, New York.

Jensen-Seaman, M. I., A. S. Deinard, and K. K. Kidd. 2003. Mitochondrial and nuclear DNA estimates of divergence between western and eastern gorillas *in* A. B. Taylor, and M. L. Goldsmith, eds. Gorilla Biology: a multidisciplinary perspective. University Press, Cambridge.

Jerison, H. J. 1973. Evolution of the brain and intelligence. Academic Press, New York.

Johnson, V. E., R. O. Deaner, and C. P. van Schaik. 2002. Bayesian analysis of rank data with application to primate intelligence experiments. Journal of the American Statistical Association 97:8-17.

Jones, K. E., and A. M. MacLarnon. 2004. Affording larger brains: Testing hypotheses of mammalian brain evolution on bats. American Naturalist 164:E20-E31.

Kappeler, P. M. 1997. Determinants of primate social organization: Comparative evidence and new insights from Malagasy lemurs. Biological Reviews of the Cambridge Philosophical Society 72:111-151.

Klopfer, P. H., and R. H. MacArthur. 1960. Niche Size and Faunal Diversity. American Naturalist 94:293-300.

Knott, C. D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. International Journal of Primatology 19:1061-1079.

Knott, C. D. 2005. Energetic Responses to Food Availability in the Great Apes: Implications for Hominin Evolution. Pp. 351-378 *in* D. A. Brockman, and C. P. van Schaik, eds. Seasonality in Primates. Cambridge University Press, New York.

Köhler, M., and S. Moyà-Solà. 2004. Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. Brain Behavior and Evolution 63:125-140.

Korstjens, A. H., K. Bergmann, C. Deffernez, M. Krebs, E. C. Nijssen, B. A. M. van Oirschot, C. Paukert, and E. P. Schippers. 2007. How small-scale differences in food competition lead to different social systems in three closely related sympatric colobines *in* W. S. McGraw, K. Zuberbühler, and R. Noe, eds. Monkeys of the Tai Forest. Cambidge University Press, Cambridge.

Krilowicz, B. L., S. F. Glotzbach, and H. C. Heller. 1988. Neuronal-Activity during Sleep and Complete Bouts of Hibernation. American Journal of Physiology 255:R1008-R1019.

Kudo, H., and R. I. M. Dunbar. 2001. Neocortex size and social network size in primates. Animal Behaviour 62:711-722.

Langer, P. 1988. The Mammalian Herbivore Stomach: Comparative Anatomy, Function and Evolution. Gustav Fischer Verlag, New York.

Langer, P. 2003. Lactation, weaning period, food quality, and digestive tract differentiations in eutheria. Evolution 57:1196-1215.

Laughlin, S. B., R. R. D. van Steveninck, and J. C. Anderson. 1998. The metabolic cost of neural information. Nature Neuroscience 1:36-41.

Leendertz, S. A. J., S. Metzger, E. Skjerve, T. Deschner, C. Boesch, J. Riedel, and F. H. Leendertz. 2010. A Longitudinal Study of Urinary Dipstick Parameters in Wild Chimpanzees (Pan troglodytes verus) in Cote d'Ivoire. American Journal of Primatology 72:689-698.

Lefebvre, L., S. M. Reader, and D. Sol. 2004. Brains, innovations and evolution in birds and primates. Brain Behavior and Evolution 63:233-246.

Lehman, S. M., M. Mayor, and P. C. Wright. 2005. Ecogeographic size variations in sifakas: A test of the resource seasonality and resource quality hypotheses. American Journal of Physical Anthropology 126:318-328.

Lindenfors, P. 2005. Neocortex evolution in primates: the 'social brain' is for females. Biology Letters 1:407-410.

Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683-1699.

Lukas, W. D., and B. C. Campbell. 2000. Evolutionary and ecological aspects of early brain malnutrition in humans. Human Nature-an Interdisciplinary Biosocial Perspective 11:1-26.

MacDonald, K. 2002. Statistical analysis of the distribution of modern primates: a comparative approach to the spatial analysis of the Palaelithic. Pp. 105-112 *in* G. Burenhult, and J. Arvidsson, eds. Archaeological informatics. BAR International Series 1016. Oxford UK: ArcheoPress.

MacLean, E. L., N. L. Barrickman, E. M. Johnson, and C. E. Wall. 2009. Sociality, ecology, and relative brain size in lemurs. Journal of Human Evolution 56:471-478.

Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary consequences of fallback foods. International Journal of Primatology 28:1218-1235.

Martin, R. D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293:57-60.

Martin, R. D. 1996. Scaling of the mammalian brain: The maternal energy hypothesis. News in Physiological Sciences 11:149-156.

Martin, R. D. 2000. Origins, diversity and relationships of lemurs. International Journal of Primatology 21:1021-1049.

Martin, R. D., M. Genoud, and C. K. Hemelrijk. 2005. Problems of allometric scaling analysis: Examples from mammalian reproductive biology. Journal of Experimental Biology 208:1731-1747.

McNab, B. K. 2002. The physiological ecology of vertebrates: a view from energetics. Cornell University Press, New York.

McNab, B. K. 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 151:5-28.

Meijaard, E., and C. P. Groves. 2004. The biogeographical evolution and phylogeny of the genus *Presbytis*. Primate Report 68:71-90.

Meiri, S., P. Raia, and A. B. Phillimore. 2011. Slaying dragons: limited evidence for unusual body size evolution on islands. Journal of Biogeography 38:89-100.

Millien, V. 2006. Morphological evolution is accelerated among island mammals. Plos Biology 4:1863-1868.

Millien, V. 2011. Mammals Evolve Faster on Smaller Islands. Evolution 65:1935-1944.

Milton, K. 1988. Foraging behaviour and the evolution of primate intelligence *in* R. W. Byrne, and A. Whiten, eds. Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. University Press, Oxford.

Mink, J. W., R. J. Blumenschine, and D. B. Adams. 1981. Ratio of central nervous system to body metabolism in vertebrates, its constancy and functional basis. American Journal of Physiology 241:R203-R212.

Mittermeier, R., J. Ganzhorn, W. Konstant, K. Glander, I. Tattersall, C. Groves, A. Rylands, A. Hapke, J. Ratsimbazafy, M. Mayor, E. E. Louis, Y. Rumpler, C. Schwitzer, and R. Rasoloarison. 2008. Lemur Diversity in Madagascar. International Journal of Primatology 29:1607-1656.

Montgomery, S. H., I. Capellini, R. A. Barton, and N. I. Mundy. 2010. Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and Homo floresiensis. Bmc Biology 8.

Myneni, R., W. T. B. Yang, N. Shabanov, and Y. Knyazikhin. 2005. Global products of vegetation leaf area and fraction absorbed PAR from MODIS sensors onboard NASA Terra and Aqua satellites. Pp. 200-202 *in* S. Liang, J. Liu, X. Li, R. Liu, and M. Schaepman, eds. Proceedings of the 9th International Symposium on Physical Measurements and Signatures in Remote Sensing, Beijing, China.

Nagy, K. A., and K. Milton. 1979. Energy-Metabolism and Food-Consumption by Wild Howler Monkeys (Alouatta-Palliata). Ecology 60:475-480.

Navarrete, A., C. P. van Schaik, and K. Isler. in rev. Energetics and the evolution of human brain size: no gut-brain trade-off in mammals.

Niven, J. E. 2005. Brain evolution: Getting better all the time? Current Biology 15:R624-R626.

Niven, J. E. 2007. Brains, islands and evolution: breaking all the rules. Trends in Ecology & Evolution 22:57-59.

Nunn, C. L. 1999. The number of males in primate social groups: a comparative test of the socioecological model. Behavioral Ecology and Sociobiology 46:1-13.

Orlando, L., S. Calvignac, C. Schnebelen, C. J. Douady, L. R. Godfrey, and C. Hanni. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. Bmc Evolutionary Biology 8:-.

Orme, D. 2011. The caper package: comparative analysis of phylogenetics and evolution in R. R package, https://r-forge.r-project.org/projects/caper/.

Orme, D., R. P. Freckleton, G. Thomas, T. Petzoldt, and S. Fritz. 2009. CAIC: Comparative Analyses using Independent Contrasts. R package version 1.0.4-94/r94, http://R-Forge.R-project.org/projects/caic.

Osterholz, M., L. Walter, and C. Roos. 2008. Phylogenetic position of the langur genera *Semnopithecus* and *Trachypithecus* among Asian colobines, and genus affiliations of their species groups. Bmc Evolutionary Biology 8:-.

Ostner, J., P. M. Kappeler, and M. Heistermann. 2002. Seasonal variation and social correlates of androgen excretion in male redfronted lemurs (*Eulemur fulvus rufus*). Behavioral Ecology and Sociobiology 52:485-495.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematic Biology 48:612-622.

Parker, S. T., and K. R. Gibson. 1979. A developmental model for the evolution of language and intelligence in early hominids. Behavioral and Brain Sciences 2:367-381.

Pastorini, J., R. D. Martin, P. Ehresmann, E. Zimmermann, and M. R. J. Forstner. 2001. Molecular phylogeny of the lemur family *cheirogaleidae* (primates) based on mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 19:45-56.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503-510.

Piersma, T. 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? Journal of Avian Biology 29:511-520.

Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. Integrative and Comparative Biology 42:51-67.

Plavcan, J. M. 2003. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: Implications for the fossil record. American Journal of Physical Anthropology 120:38-60.

Plavcan, J. M., and C. P. van Schaik. 1992. Intrasexual Competition and Canine Dimorphism in Anthropoid Primates. American Journal of Physical Anthropology 87:461-477.

Plavcan, J. M., C. P. van Schaik, and W. S. McGraw. 2005. Seasonality, Social Organization, and Sexual Dimorphism in Primates. Pp. 401-442 *in* D. A. Brockman, and C. P. Van Schaik, eds. Seasonality in Primates. Cambridge University Press, New York.

Pontzer, H., D. A. Raichlen, R. W. Shumaker, C. Ocobock, and S. A. Wich. 2010. Metabolic adaptation for low energy throughput in orangutans. Proceedings of the National Academy of Sciences of the United States of America 107:14048-14052.

R-Development-Core-Team. 2010. R: A language and environment for statistical computing, R Foundation for Statistical Computing. Vienna, Austria.

Raia, P., and S. Meiri. 2011. The Tempo and Mode of Evolution: Body Sizes of Island Mammals. Evolution 65:1927-1934.

Reader, S. M., Y. Hager, and K. N. Laland. 2011. The evolution of primate general and cultural intelligence. Philosophical Transactions of the Royal Society B-Biological Sciences 366:1017-1027.

Reader, S. M., and K. N. Laland. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences of the United States of America 99:4436-4441.

Reader, S. M., and K. MacDonald. 2003. Environmental variability and primate behavioural flexibility. Pp. 83-116 *in* S. M. Reader, and K. N. Laland, eds. Animal Innovation. Oxford University Press.

Richard, A. F., and R. E. Dewar. 1991. Lemur Ecology. Annual Review of Ecology and Systematics 22:145-175.

Richards, S. A. 2005. Testing ecological theory using the information-theoretic approach: Examples and cautionary results. Ecology 86:2805-2814.

Rowe, N. 1996. The pictorial guide to the living primates. Pogonias Press, New york.

Sacher, G. 1959. Relation of lifespan to brain weight and body weight in mammals. Pp. 115-133 *in* G. E. W. Wolstenholme, and M. O'Connor, eds. The Lifespan of Animals. Churchill, London.

Safi, K., M. A. Seid, and D. K. N. Dechmann. 2005. Bigger is not always better: when brains get smaller. Biology Letters 1:283-286.

Sawaguchi, T. 1992. The size of the neocortex in relation to ecology and social structure in monkeys and apes. Folia Primatologica 58:131-145.

Schmid, J. 1999. Sex-specific differences in activity patterns and fattening in the gray mouse lemur (Microcebus murinus) in Madagascar. Journal of Mammalogy 80:749-757.

Schmid, J., and J. R. Speakman. 2000. Daily energy expenditure of the grey mouse lemur (Microcebus murinus): a small primate that uses torpor. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 170:633-641.

Schuck-Paim, C., W. J. Alonso, and E. B. Ottoni. 2008. Cognition in an ever-changing world: Climatic variability is associated with brain size in neotropical parrots. Brain Behavior and Evolution 71:200-215.

Schülke, O., and J. Ostner. 2007. Physiological ecology of *cheirogaleid* primates: variation in hibernation and torpor. Acta Ethologica 10:13-21.

Schwartz, G., P. Mahoney, L. Godfrey, and W. Jungers. 2005. Dental development and life history in one of the largest subfossil Malagasy lemurs, *Megaladapis edwardsi*. Journal of Vertebrate Paleontology 25:111a-112a.

Shultz, S., R. B. Bradbury, K. L. Evans, R. D. Gregory, and T. M. Blackburn. 2005. Brain size and resource specialization predict long-term population trends in British birds. Proceedings of the Royal Society B-Biological Sciences 272:2305-2311.

Shultz, S., and R. I. M. Dunbar. 2006. Both social and ecological factors predict ungulate brain size. Proceedings of the Royal Society B-Biological Sciences 273:207-215.

Shultz, S., and R. I. M. Dunbar. 2007. The evolution of the social brain: anthropoid primates contrast with other vertebrates. Proceedings of the Royal Society B-Biological Sciences 274:2429-2436.

Smith, R. J., and J. M. Cheverud. 2002. Scaling of sexual dimorphism in body mass: A phylogenetic analysis of Rensch's rule in primates. International Journal of Primatology 23:1095-1135.

Smith, R. J., and W. L. Jungers. 1997. Body mass in comparative primatology. Journal of Human Evolution 32:523-559.

Sol, D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biology Letters 5:130-133.

Sol, D., S. Bacher, S. M. Reader, and L. Lefebvre. 2008. Brain size predicts the success of mammal species introduced into novel environments. American Naturalist 172:S63-S71.

Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005a. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America 102:5460-5465.

Sol, D., N. Garcia, A. Iwaniuk, K. Davis, A. Meade, W. A. Boyle, and T. Szekely. 2010. Evolutionary divergence in brain size between migratory and resident birds. PLoS ONE 5:e9617.

Sol, D., and L. Lefebvre. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90:599-605.

Sol, D., L. Lefebvre, and J. D. Rodriguez-Teijeiro. 2005b. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proceedings of the Royal Society B-Biological Sciences 272:1433-1441.

Sol, D., T. Szekely, A. Liker, and L. Lefebvre. 2007. Big-brained birds survive better in nature. Proceedings of the Royal Society B-Biological Sciences 274:763-769.

Sterling, E. J. 1994. Evidence for Nonseasonal Reproduction in Wild Aye-Ayes (*Daubentonia madagascariensis*). Folia Primatologica 62:46-53.

Strier, K. B., T. E. Ziegler, and D. J. Wittwer. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). Hormones and Behavior 35:125-134.

Taylor, A. B., and C. P. van Schaik. 2007. Variation in brain size and ecology in *Pongo*. Journal of Human Evolution 52:59-71.

Terborgh, J. 1983. Five New World Primates. Princeton University Press, Princeton.

Tomasello, M. 1999. The cultural origins of human cognition. Harvard University Press, Cambridge, MA.

Tsuji, Y., N. Kazahari, M. Kitahara, and S. Takatsuki. 2008. A more detailed seasonal division of the energy balance and the protein balance of Japanese macaques (Macaca fuscata) on Kinkazan Island, northern Japan. Primates 49:157-160.

Tucker, C. J., J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote, and N. El Saleous. 2005. An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. International Journal of Remote Sensing 26:4485-4498.

van Schaik, C. P., and K. R. Pfannes. 2005. Tropical Climates and Phenology: a Primate Perspective. Pp. 23-54 *in* D. A. Brockman, and C. P. van Schaik, eds. Seasonality in Primates. Cambridge University Press, New York.

van Woerden, J. T., C. P. van Schaik, and K. Isler. 2010. Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. American Naturalist 176:758-767.

van Woerden, J. T., C. P. van Schaik, and K. Isler. 2011. Large brains buffer energetic effects of seasonal habitats in catarrhine primates. Evolution in Press.

Vogel, E. R., J. T. van Woerden, P. W. Lucas, S. S. U. Atmoko, C. P. van Schaik, and N. J. Dominy. 2008. Functional ecology and evolution of hominoid molar enamel thickness: Pan troglodytes schweinfurthii and Pongo pygmaeus wurmbii. Journal of Human Evolution 55:60-74.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh.

Weston, E. M., and A. M. Lister. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. Nature 459:85-U88.

Whiten, A., and R. W. Byrne. 1997. Machiavellian Intelligence II. Extensions and Evaluations. Cambridge University Press, Cambridge.

Winkler, H., B. Leisler, and G. Bernroider. 2004. Ecological constraints on the evolution of avian brains. Journal of Ornithology 145:238-244.

Wolda, H. 1978. Fluctuations in Abundance of Tropical Insects. American Naturalist 112:1017-1045.

Wright, P. C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Yearbook of Physical Anthropology 1999, Vol 42 42:31-72.

Wright, S. J., and C. P. van Schaik. 1994. Light and the Phenology of Tropical Trees. American Naturalist 143:192-199.

Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. American Journal of Physical Anthropology 106:283-295.